Ancient chemosynthetic bivalves: systematics of Solemyidae from eastern and southern Australia (Mollusca: Bivalvia)

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ABSTRACT

The systematics of the chemosymbiotic bivalve mollusc family Solemyidae in Australia are reviewed using morphological characters and some molecular data. Recognised world genera/subgenera are redefined on the basis of ligament characters and features of the posterior aperture and an additional new subgenus *Solemya (Austrosolemya)* (type species *S. australis*) is proposed. Four species are recognised from eastern Australia, including three from Moreton Bay: *S. (Solemyarina) terraereginae*, *S (S.) velesiana*, and *Solemya moretonensis* sp. nov., with another undescribed species represented by a single specimen from Moreton Bay. The large *Solemya (Austrosolemya) australis* is distributed around southern and southwestern Australia while two further species, from South and Western Australia, are recognised on the basis of molecular data and to some extent morphology, but not formally named. For the first time, major features of the anatomy, including details of ctenidia and bacteriocytes, of an Australian solemyid (*S. (Solemyarina) velesiana*) are described. ❑ *taxonomy, revision, new species, Solemya Moreton Bay, chemosynthesis*

The Solemyidae is one of five bivalve families known to possess endosymbioses with sulphide-oxidising, chemoautotrophic bacteria housed in the gills (Fisher 1990; Distel 1998; Stewart & Cavanaugh 2006). Morphologically, Solemyidae are highly distinctive and unusual bivalves, with an elongate, near cylindrical shape and covered with glossy, thick, brown periostracum extended as a broad, pleated, flexible fringe. They have thin, lightly calcified, organic-rich, flexible, edentulous shells, with extensive ventral mantle fusion forming a large anterior aperture, through which protrudes the large, papillae-fringed foot, and a small posterior aperture. Large ctenidia occupy most of posterior mantle cavity and the gut is much reduced, or absent in some species. Solemyids are also capable of swimming by jet propulsion by expulsion of water through the posterior aperture (Reid 1980).

All species investigated in any detail possess endosymbionts (Kreuger & Cavanaugh 1997). Likely vertical transmission of symbionts through eggs is known for *Solemya velum* (Kreuger *et al.* 1996). The biology of the chemosymbiosis of solemyids has been much studied with the north American *Solemya velum* Say, 1822 and the gutless species, *Solemya reidi* Bernard, 1980, attracting most attention (Reid 1980; Powell & Somero 1985; Fisher & Childress 1986; Gustafson & Reid 1986; Conway *et al.* 1989; Stewart & Cavanaugh 2006). While a number of solemyids characteristically have small or reduced

alimentary systems (Stempell 1899; Owen 1961; Kuznetsov *et al.* 1990; Reid 1998), the gutless condition is known in *Acharax alinae* Métivier & Cosel, 1993, *Petrasma atacama* Kuznetzov & Schileyko, 1984, *Acharax eremita* Kuznetsov & Schileyko, 1984, and *Petrasma borealis* (Totten, 1834) (see Kuznetzov & Schileyko 1984; Conway *et al.* 1992; Métivier & Cosel 1993).

There are around 30 described species in the family, although it is certain that there are undescribed species from deepwater cold seeps (see Neulinger *et al.* 2006) as well as unregarded small species in tropical shallow waters. Most shallow water solemyids are small, with lengths of less than 30 mm, but *Acharax* species from deeper water attain larger sizes — *Acharax bartschii* Dall, 1908 reaches 210 mm shell length, *Acharax alinae* 135 mm (Métivier & Cosel 1993) while a fossil *Acharax* from the Miocene measured a massive 300 mm (Kanie & Kuramochi 1995).

Solemyids are geographically widespread from the tropics to temperate latitudes and with a depth range from the intertidal to 5350 m (Fujiwara 2003). They inhabit muds, silts and sands (Stanley 1970; Conway *et al.* 1992; Krueger *et al.* 1996) but are often associated with organically enriched habitats such as seagrass beds (Stanley 1970; Reid & Brand 1987), wood pulp accumulations (Reid 1980), human hair in sewage dumps (Coan *et al.* 2000), and deep-sea cold seeps and vents (Métivier & Cosel 1993; Neulinger *et al.* 2006).

Solemyidae are probably geologically the oldest of the chemosymbiotic bivalves with a fossil record extending back into the Lower Palaeozoic. The earliest known is *Ovatoconcha* from the early Ordovician (Arenig ca 475 mya) (Cope 1996a), while other solemyids are known from the middle Ordovician and younger rocks (Pojeta 1988). The general similarity in morphology of these fossils to living species suggests that they possessed similar life habits.

In view of their life habits and antiquity, the relationships of solemyids to other bivalves are of considerable interest. Most classifications place the Solemyidae along with the Manzanellidae (=Nucinellidae) in the superfamily Solemyoidea, and together with the Nuculoidea and Nuculanoidea in the subclass Protobranchia, occupying a basal position relative to all other bivalves (Yonge 1939; Pojeta 1988; Starobogatov 1992; Morton 1996; Cope 2000; Zardus 2002). Alternatively, some classifications suggest placement of Solemyoidea in a separate subclass (Cox 1969; Cope 1996b; Amler 1999). Cladistic analyses of morphological characters have grouped Solemyidae and Nuculidae as sister taxa within the subclass Protobranchia (Salvini-Plawen & Steiner 1996; Waller 1998; Giribet & Wheeler 2002). Molecular evidence indicates that either Solemyidae form a monophyletic group (weakly supported) with Nuculidae and Nuculanoidea (Steiner & Hammer 2000) or, alternatively, Solemyidae and Nuculidae group as sister taxa but are distinct from Nuculanoidea and the rest of the bivalves (Giribet & Distel 2004, fig. 3.6). In this latter analysis, the clade Solemyidae + Nuculidae groups with other conchiferan classes Gastropoda, Scaphopoda and Cephalopoda rather than with the rest of the bivalves that form a monophyletic clade.

Despite the biological interest of solemyids, their systematics is confused with species appearing very similar to each other on external characters. Internally, there are differences in the morphology of the hinge and ligament, such that ligamental characters have been used as a basis for subgeneric and generic separation but interpretations have differed (Dall 1908a,b; Cox 1969; Bernard 1980; Lamprell & Healy 1998). There has been no attempt to incorporate anatomical characters into systematics although some prominent features such as the posterior pallial apertures are potentially character-rich. Molecular data are desirable for future systematic studies of Solemyidae but, as yet, few species have been analysed (Giribet & Distel 2004; Neulinger *et al.* 2006).

AUSTRALIAN SPECIES

Three species of Solemyidae have been described from Australia: *Solemya australis* Lamarck, 1818, from south western Australia; *S. terraereginae* Iredale, 1929, from Queensland and *S. velesiana* Iredale, 1931, from New South Wales. Inexplicably, Lamprell & Healy (1998) synonymised the tropical *S. terraereginae* with *S. australis* from southern Australia, with this decision followed in other publications, e.g. the Database of Indo-Pacific Marine Molluscs <http://data.acnatsci.org/obis/search.php>. They

also placed *Solemya australis* and *S. velesiana* into separate subgenera *Solemya* s.s. and *Solemyarina*.

Symbiotic bacteria were first recorded in the gills of *Solemya velesiana* and *S. australis* by Reid & Brand (1987) who also provide some anatomical information for the two species. Their samples of *S. velesiana* came from Orpheus I., Queensland and they may have confused the species with *S. terraereginae*. Both small and large solemyids from southern and western Australia were referred to *S. australis* but it seems likely that at least two species have been confounded. Later, Kreuger & Cavanaugh (1997) sequenced the bacterial symbionts of *S. terraereginae* from Lizard Island and gave TEM details of their location in the gill filaments.

From samples collected during the Marine Biological Workshop in Moreton Bay, we recognised three small *Solemya* species; one was regularly encountered in sediment from intertidal seagrass habitats; another smaller species was recovered from slightly deeper water grab samples outside the Bay and a third was represented by only a single specimen, again from a grab sample, but within the Bay. In attempting to identify these bivalves and samples from two other sites in South and Western Australia it became apparent that the systematics of Solemyidae from Australia needed some updating for the original descriptions and illustrations of the described species were poor.

In this paper we review the systematics of Australian Solemyidae, provide new illustrations of the relevant type material, identify the Moreton Bay species and discuss the status of other small solemyids from Australia. We also review the characters of living solemyid genera providing new illustrations of ligament and apertural characters. We present new molecular sequences of 18S and 28S rRNA and cytochrome B genes for the most abundant of the Moreton Bay species and compare them with sequences from other putative species collected in South and Western Australia and with published sequences from other *Solemya* from North America and *Acharax* spp. from deeper water. Additionally, we provide details of the anatomy of *Solemya velesiana* from Moreton Bay and compare it with other *Solemya* species from Australia and elsewhere.

MATERIAL AND METHODS

COLLECTION OF SAMPLES AND HABITATS

Queensland Moreton Bay. *Solemya (Solemyarina) velesiana* was sieved from intertidal seagrass-covered sand between Dunwich and Amity Point, North Stradbroke Island, Moreton Bay in February 2005. A single specimen of another unnamed species was dredged from mud at Banana Bank in southern Moreton Bay. *Solemya moretonensis sp. nov.* was obtained from grab samples seaward of Moreton Island.

Queensland, Lizard Island. *S. (Solemyarina) terraereginae* was sieved from intertidal lagoon sands with a sparse covering of the seagrass *Halophila* in November 2000.

South Australia. A sample of the small solemyid *S. (Solemyarina)* species A was collected intertidally from a narrow, silt covered, rock platform at Anchorage Bay, Victor Harbor, South Australia in February 2001.

Western Australia. Three small individuals of *S. (Solemyarina)* species B were sieved from mud covered in dead algae, in a mangrove-fringed channel, at Little Lagoon, Denham, Shark Bay in July 2004.

ANATOMY

General anatomy of specimens from Moreton Bay and Lizard Island was studied by serial thin sections of decalcified, formalin-fixed specimens. Sections were cut at 8 mm and stained with Masson's trichrome. For examination of the ligaments, hinge areas of the solemyids were dissected from the shell and imaged beneath ethanol with transmitted light. For scanning electron microscopy, animals were fixed in a 2.5% solution of glutaraldehyde in phosphate buffer or 5% formalin in seawater. The animals were dissected and the tissues sliced with a razor blade. Tissue pieces were then dehydrated through ascending concentrations of acetone, critical point dried, mounted on stubs, coated with gold and examined by SEM (Philips FE X30).

DNA EXTRACTION, AMPLIFICATION AND SEQUENCING.

Animals for molecular analysis were preserved in absolute ethanol. DNA was extracted and portions of two genes, the nuclear 18S rRNA and 28S rRNA genes, were amplified and sequenced following the methods of Williams

& Ozawa (2006). One sequence of the mitochondrial cytochrome B (cytB) gene was obtained from each Australian *Solemya* sample using primers cytb-F (GRGGKGCTACKGTAATTACTAA) and cytb-R (AAATAYCAYTCNGGCTGRATATG), following the amplification conditions for COI in Williams & Ozawa (2006). Sequence reactions were performed directly on purified PCR products using a BigDye Terminator v1.1 Cycle Sequencing Kit (Applied Biosystems) and run on an Applied Biosystems 3730 DNA Analyser automated capillary sequencer. Sequences were verified by forward and reverse comparisons.

Sequences were edited and aligned following methods in our previous studies (Williams *et al.* 2004; Taylor *et al.* 2005). Poorly aligned sites were identified using Gblocks (0.19b, Castresana 2000) and removed from analyses. After removal of ambiguous blocks of data, a total of 920 bp of sequence from 18S rRNA remained to be used in phylogenetic analyses of the large taxon set (90% of 1013 bp in the original alignment) and 1469 bp of 28S rRNA (99% of 1477 bp in the original alignment). The alignment of cytB was unambiguous. Pairwise distances were calculated among the three cytB sequences using Kimura's 2-parameter (Kimura 1980) distance.

Phylogenies were constructed for the nuclear genes using maximum likelihood (ML) as implemented in PAUP* (Swofford 2002). The models used were K80+ G (t ratio = 2.0331, α = 0.1928) for 18S rRNA and GTR+G (Base sequences = (0.2324, 0.2543, 0.3124) Nst = 6 Rmat=(0.8306, 1.4938, 0.9609, 0.5928, 5.5177) α = 0.2479) for 28S rRNA, which were among several options suggested by MrModelTest (v 2.1, J. Nylander (http://www.abc.se/~nylander/). Taxa were added randomly with ten replicates and a heuristic search option used with nearest neighbour interchange (NNI) branch-swapping. On completion of this analysis, it was repeated using the tree obtained from the first search, and tree bisection-reconnection (TBR) branch-swapping. Nodal support was tested by bootstrapping with ML with ten random replicates of taxa, TBR branch-swapping and with neighbour-joining bootstrap (NJ) using ML distances, both with 1,000 replicates.

Voucher material of the sequenced species is lodged in the Natural History Museum, London, registration numbers 20060149–152.

ABBREVIATIONS

AMS, Australian Museum, Sydney; BMNH, Natural History Museum, London; MNHN, Museum National d'Histoire Naturelle, Paris; QM, Queensland Museum, Brisbane; WAM, Western Australian Museum Perth.

SYSTEMATICS

Identification and classification of solemyid species has proven especially troublesome because of the overall similarity of external shell features within the group, coupled with the delicate fragile shells, thick, brown periostracum and the lack of standard bivalve features such as shell sculpture and hinge teeth. Most 20th century authors used characters of the internal ligament in an attempt to define suprageneric groupings. Dall (1908a, b) was the first to recognise differences in ligament morphology amongst solemyids and proposed a subgeneric classification of *Solemya* species based largely on the structure of the ligament and supporting calcified structures. He defined *Solemya* s.s. as having internal lateral ligament extensions located anterior to the chondrophore and the subgenus *Petrasma* with the ligament not exposed internally anterior to the chondrophore, while *Acharax* has an external ligament. However, his concept of *Solemya sensu stricto* was based on *S. australis* rather than *S. togata* (Poli, 1795) as the type species and the two taxa are very different in ligament structure, the latter lacking the anterior lateral extensions as lobate or linear structures.

Later, Iredale introduced two more genera; *Solemyarina* Iredale, 1931 (type *S. velesiana*) and *Zesolemya* Iredale, 1939 (type *S. parkinsonii*), also based on the structure of the ligament, but his diagnoses were very brief. Cox (1969) unraveled much of the confusion and correctly illustrated the ligament of *S. togata* as the type species of *Solemya*. Unfortunately, the ligament of *S. australis* was illustrated as the type of *Solemyarina* rather than *S. velesiana*. Further confusion was added by Bernard (1980, figs 1–3) who classified *Solemya reidi* into *Solemya*, despite the anterior lateral extensions. Confusion has continued with Lamprell & Healy (1998) also placing *S. australis* in *Solemya s. s.*

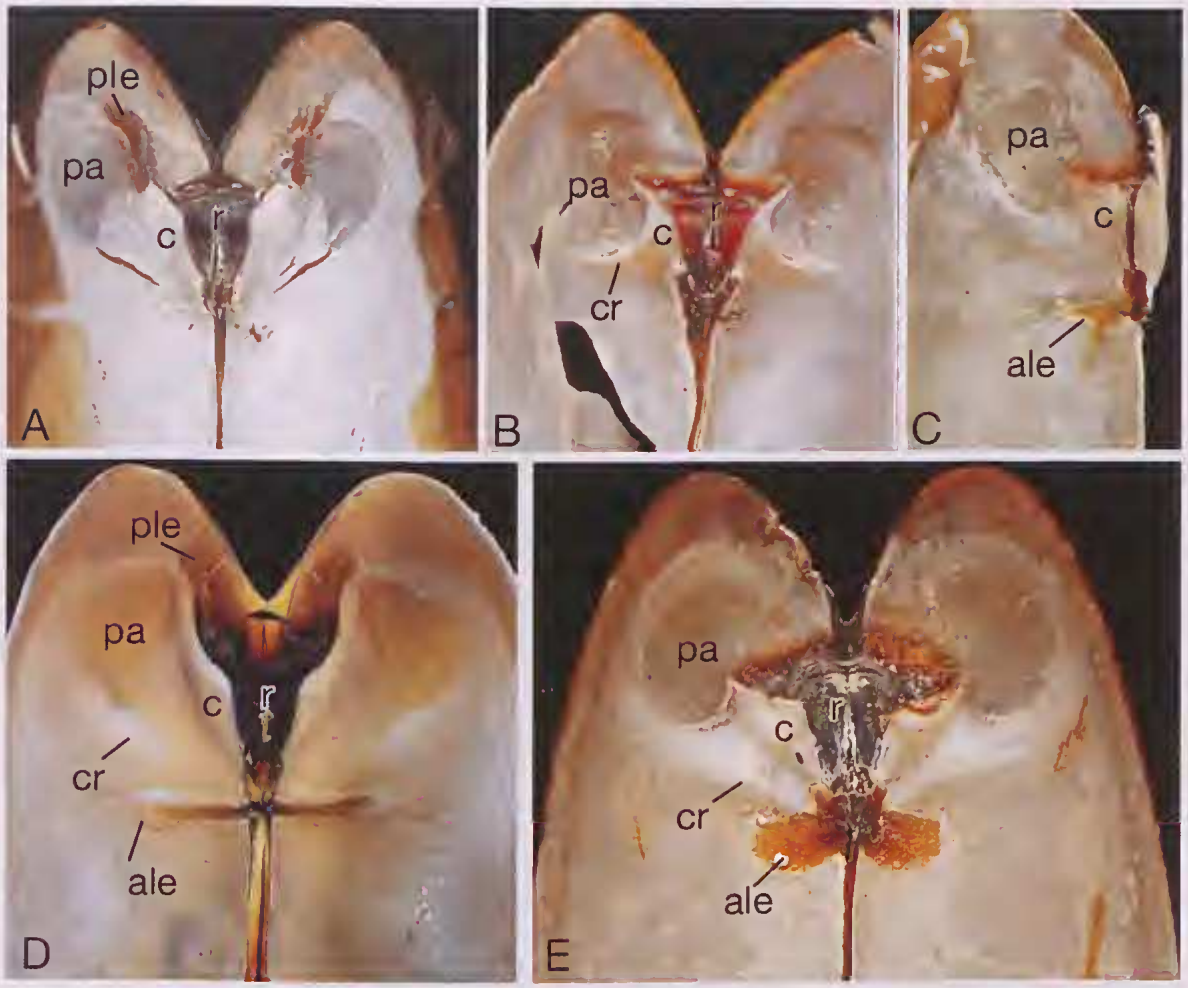


FIG. 1. Internal ligamental areas of type species of genera and subgenera of Solemyidae. **A**, *Solemya*: *Solemya togata*, Malta (BMNH-78.5.10.220); **B**, *Petrasma*: *S. (Petrasma) velum*, Narragansett, Rhode Island, USA (used as a proxy for *S. borealis* as no material suitable for imaging available); **C**, *Solemyarina*: *S. velesiana*, Port Jackson, Sydney (BMNH-95.3.7.17–19); **D**, *Zesolemya*: *S. parkinsonii* (syntype BMNH-1852.3.16.46–48), New Zealand; **E**, *Austrosolemya*: *Solemya australis* (often incorrectly illustrated as the type of *Solemya* s.s.), Australia, Cuming Collection (BMNH). ale = anterior lateral extension; c = chondrophore; cr = chondrophoral ridge; pa = posterior adductor scar; ple = posterior ligament extension; r = resilifer. Scale bars: A, D, E = 5 mm; B, C = 2 mm.

Below we list the currently accepted genera and subgenera of Solemyidae with a brief summary of their ligament characters. Figure 1 shows the main features of the ligament in these taxa. Additionally, our observations suggest that characters of the posterior aperture, such as numbers and arrangement of papillae may have some potential in solemyid systematics, as originally observed by Morse (1913) in *Solemya velum* and *S. borealis*. We also include brief descriptions and illustrations of these based on type species of the genera. Following Stempell (1899), the apertural papillae can be described in two groups — the dorsal, suprasiphonal papillae are paired and located above or at the dorsal margin of the aperture, with in most species, a single papilla located dorso-centrally (Fig. 2A–G); siphonal papillae either totally surround the aperture or just fringe the ventral margin. The suprasiphonal papillae are often larger than the siphonal papillae with the ventral pair always longer.

For the present, and pending further analysis, we regard *Solemyarina, Petrasma, Zesolemya* and *Austrosolemya* as subgenera of *Solemya*.

Solemya Lamarck, 1818

Type species: *S. mediterranea* (Lamarck 1818) = *Tellina togata* Poli, 1795 (by subsequent designation Children, 1823)

Remarks. The chondrophore is large (Fig. 1A) with a broad, triangular resilium and supporting ribs around the posterior adductor are absent. Narrow strips of ligament are visible along both ventral edges of chondrophore and anterior lateral extensions of ligament are absent. Posteriorly, the outer ligament layer extends as two narrow tongues around the dorsal

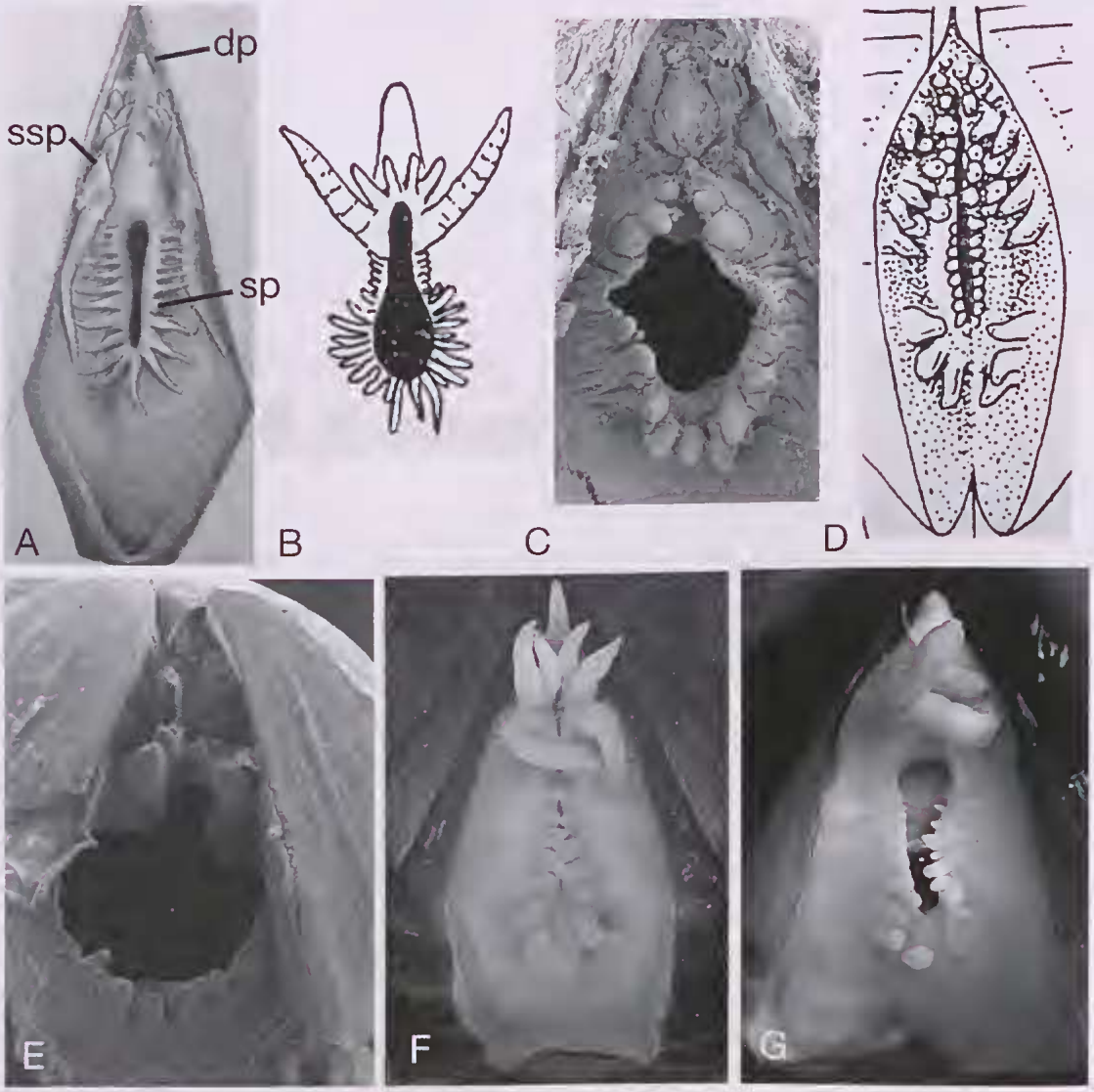


FIG. 2. Posterior apertures of Solemyidae: type species of subgenera. **A**, *Solemya*: *S. togata* (from Stempell, 1899, fig. 2); **B**, *Petrasma*: *Solemya borealis* (from Morse 1913, fig. 21; **C**, *Petrasma velum*, Cape Cod, USA (original); **D**, *Acharax*: proxy for type species *A. eremita* (from Kuznetsov & Schileyko, 1984 fig. 3b); **E**, *Solemyarina*: *S. velesiana*, Moreton Bay (original); **F**, *Zesolemya*: *Z. parkinsonii* (from Beedham & Owen, 1965, pl. 1, fig. 2); **G**, *Austrosolemya*: *A. australis*, Esperance (original). dp = dorsal papilla; ssp = suprasiphonal papillae; sp = siphonal papillae. Scale bars: A, F, G = 5 mm; C = 2 mm; E = 0.5 mm; B, D, none given in original publication.

edge of the adductor scars (Fig. 1A). Stempell's (1899 fig. 2) figure of the posterior aperture *S. togata* shows (Fig. 2A) a single unpaired posterior papilla, seven pairs of suprasiphonal papillae, with the most ventral of these very long and slender. The siphonal opening is fringed by 20–22 pointed, slender papillae that are slightly longer on the ventral margin.

Solemya (Solemyarina) Iredale, 1931

Type species: *Solemya velesiana* Iredale, 1931 (by original designation).

Remarks. The genus was originally proposed to separate smaller eastern Australian species – *S. terraereginae* and *S. velesiana* from *Solemya*. The dorsal margins of the chondrophore are almost parallel (Fig. 1C) with a narrow resilium. The posterior margin of the chondrophore is slightly sinuous and not extended posteriorly. A low, thin chondrophoral rib extends around the anterior margin of the posterior adductor scar. The ligament anterior to the chondrophore forms a broadened, heart-shaped area, with narrow, linear, lateral extensions (Fig. 1C). The posterior aperture of *S. velesiana* (Fig. 2E) has a single, short dorsal papilla, three to four pairs of short, suprasiphonal papillae, with the ventral pair slightly larger, and 9–10 short siphonal papillae around the ventral margin, with the most ventral of these slightly larger.

Solemya (Austrosolemya) **subgen. nov.**

Type species: *Solemya australis* Lamarck, 1818 (here designated).

Remarks. For details see below under Australian species.

Solemya (Petrasma) Dall, 1908

Type species: *Solemya borealis* Totten, 1834 (by original designation), northwestern Atlantic.

Remarks. The chondrophore (Fig. 1B) has posterior and anterior supporting ridges that form an arcuate cavity around antero-dorsal margin of the posterior adductor muscle. The resilium is broad and triangular. Anterior lateral extensions of ligament are absent (Fig. 1B). The only illustration of the posterior aperture of *S. borealis* available is a sketch by Morse (1913 fig. 21). This shows (Fig. 2B) three pairs of suprasiphonal papillae, with the ventral pair long; the aperture is fringed by about 30 shorter siphonal papillae that are larger ventrally. *Solemya (Petrasama) velum*, often taken as a proxy for the type species, has similar ligament characters to *S. borealis* but the suprasiphonal papillae are shorter (Fig. 2C).

Solemya (Zesolemya) Iredale, 1939.

Type species: *Solemya parkinsonii* Smith, 1874 (by original designation), New Zealand. (Usually synonymised with *Solemyarina* (Cox, 1969) or *Solemya* (Bernard, 1980)

Remarks. Iredale distinguished *Zesolemya* from Australian *Solemyarina* species on basis of narrow posterior extensions of the ligament (Fig. 1 D plc) and the chondrophore bifurcating around the posterior adductor scar. Also, the dorsal extension of the chondrophore reaches the posterior margin of the adductor scar (Fig. 1D). Prominent anterior, lateral, linear extensions of the ligament are present (Fig. 1D ale). Based on Beedham & Owen's figure (1965, pl. 1, fig. 2) there are 3–4 pairs of long suprasiphonal papillae, the longest ventral, with around 20 large siphonal papillae that are longer ventrally (Fig. 2F).

Acharax Dall, 1908

Type species: *Solemya johnsoni* Dall, 1891 (by original designation). NE Pacific.

Remarks. The chondrophore (not figured but see Pojeta, 1988, plate 2, figs 2–5) is narrow and does not bifurcate but the shell is thickened around the posterior adductor scar. The ligament does not extend internally. The only illustration available of a posterior aperture is for *Acharax eremita* (Kuznetsov & Schileyko, 1984: fig. 3B) and this is far more complex than any *Solemya* species (Fig. 2D). There are three rows of paired suprasiphonal papillae; the inner margin of the aperture is fringed with short, siphonal papillae and six larger papillae lie ventral to the aperture.

THE AUSTRALIAN SPECIES

In this section we review the Australian species. Adult *S. (Austrosolemya) australis* can be easily recognised by their larger size, but smaller species are less readily distinguished by external shell characters. Thus, in the brief descriptions below, we focus on ligament structure and characters of the posterior aperture. Pending a

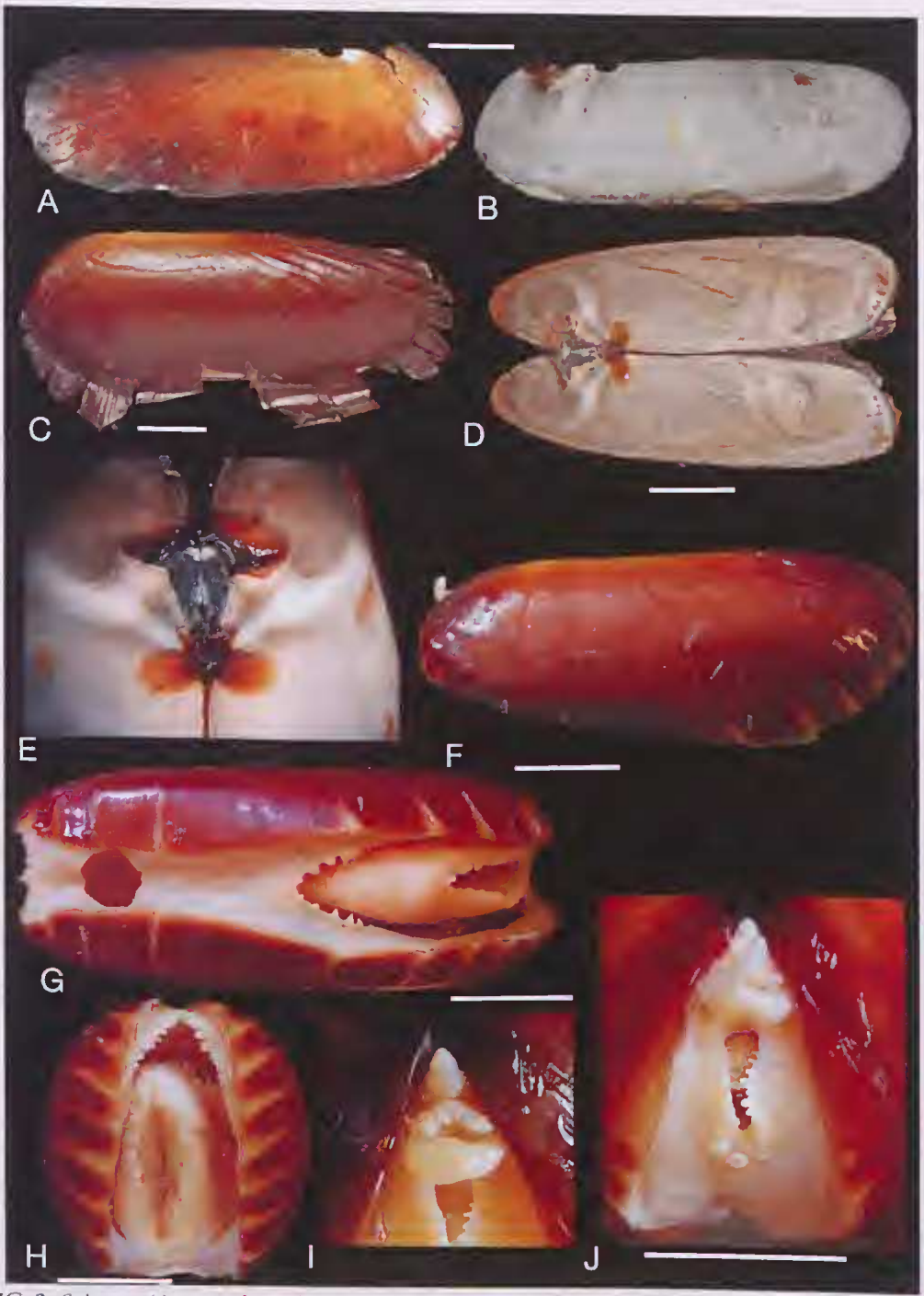


FIG. 3. *Solemya (Austrosolemya) australis* (Lamarck, 1818). **A–B**, syntype, King George Sound, Albany, Western Australia (MNHN). **C**, right side, Australia (MacAndrew Collection, BMNH); **D**, shell interior, Australia (Cuming Collection, BMNH); **E**, detail of internal ligamental area (BMNH); **F–J**, Dempster Head, Esperance, Western Australia (WAM -S16037); **F**, right lateral view; **G**, ventral view, circular hole in mantle is an artifact; **H**, anterior view showing papillae of dorsal pedal gape; **I**, dorsal and suprasiphonal papillae; **J**, posterior aperture with suprasiphonal and siphonal papillae. Scale bars = 10 mm.

global revision of the Solemyidae we classify the species within subgeneric divisions of *Solemya*.

Solemya (*Austrosolemya*) subgen. nov.

Type Species: *Solemya australis* Lamarck,1818

Diagnosis. Large *Solemya* with internal ligament possessing lobate anterior extensions, a broad triangular resilium and strong chondrophoral ridges. (Fig. 1E).

Remarks. Another included species might be *Solemya reidi* Bernard, 1980, that has a similar ligament structure (Bernard 1980, fig. 1; Coan *et al*. 2000, fig. on p. 64).

Etymology. From *australis* meaning southern

Solemya (Austrosolemya) australis Lamarck, 1818
(Figs 3 A–J)

Solemya australis Lamarck, 1818: 489.
Solemya australis – Cotton & Godfrey, 1938: 28, fig. 4.
Solemya (Solemya) australis – Lamprell & Healy, 1998: 42, fig. 48.

Material Examined. SYNTYPE: left valve, length 51 mm, King George Sound, Albany, Western Australia (on label - Port Roi George) (MNHN). OTHER MATERIAL: Victoria: Portland (AMS C92892); South Australia: Adelaide (BMNH 88.2.29.207), Glenelg (AMS C92893); Largs (AMS C92891), Holdfast Bay (AMS C47078); Kangaroo I. (AMS C143993); Spencer Gulf (AMS); West Beach (AMS). Western Australia: Esperance (WAM); Albany, Middleton Beach (AMS C 71447); Fremantle (WAM); Rottnest I. (WAM).

Description. Shell large, to 60 mm, dorsal and ventral margins sub-parallel. Periostracum thick, chestnut brown, with conspicuous raised, brown rays. Darts within periostracal pleats, cream coloured. Internal ligament, relatively short, dorsal edges of chondrophore diverging posteriorly to accommodate thick pad of inner ligament, posterior edge of chondrophore sinuate; chondrophoral buttress prominent around anterior margin of adductor muscle; anterior of ligament with subcircular lateral extensions (Figs 1E; 3E). Posterior aperture (Figs 3I, J) with a large, dorsal papilla, three pairs of suprasiphonal papillae, the ventral pair much longer and thicker, and up to 20 siphonal papillae that are larger around the ventral margin.

Distribution. Southern Australia – Victoria to Fremantle and Rottnest Island

Remarks. We are uncertain of the relationship of this species to the east coast *Solemyarina*. *S. (A.) australis* is much larger than any of the east coast species and the ligament differs in having a broadly triangular resilium, prominent, lobate, anterior lateral ligament extensions (Figs 1E, 3E) and a massive projection of the chondrophore forming a ridge round the anterior margin of the adductor muscle. The posterior aperture has larger and more numerous papillae (Figs 2G, 3 I, J).

Solemya (Solemyarina) velesiana Iredale, 1931
(Figs 4A–H)

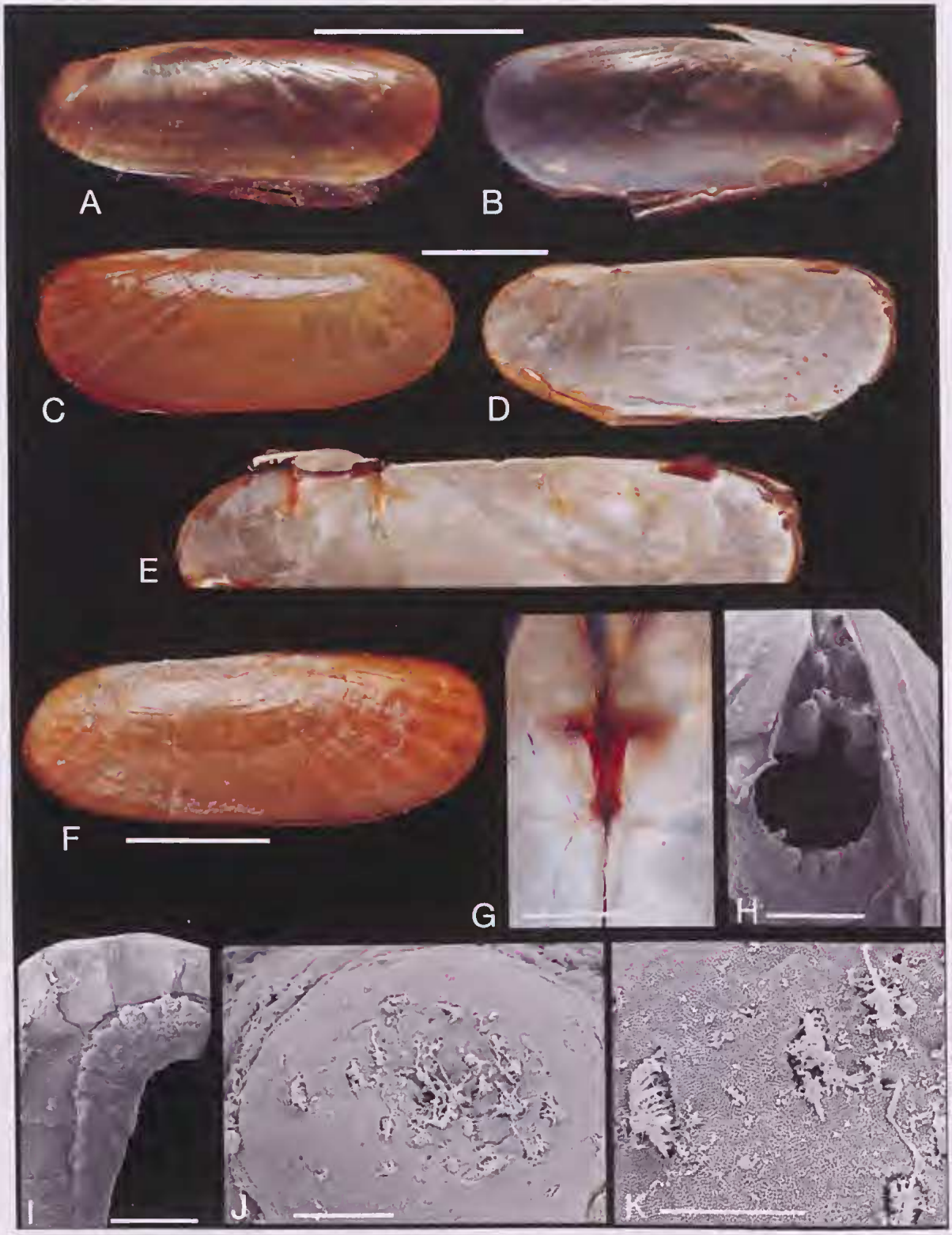
Solemya velesiana Iredale, 1931: 201. (not figured).
Solemyarina velesiana – Iredale, 1931: 202.

Material Examined. HOLOTYPE: East side of the Spit, Middle Harbour, Sydney New South Wales (AMS C7476). Length 9.5 mm. Described from Sydney area, without specific locality, but Sydney Harbour written on label – not Green I. as cited in Reid & Brand (1987: 42). OTHER MATERIAL: Queensland. North Stradbroke I., Moreton Bay (BMNH); New South Wales. Sydney Harbour (BMNH 95.3.7.17-19); Green I., Jervis Bay (AMS); Broulee (AMS); Twofold Bay (AMS). Victoria. Portsea, Port Philip Bay (AMS); South Australia. (cf *velesiana*) Kangaroo I. (AMS).

Description. Small, length to 16 mm, elongate, slightly broader anteriorly, periostracum pale brown with around six anterior and posterior white rays, corresponding to raised ridges on shell, visible through periostracum. Internal ligament with dorsal edges of chondrophore parallel and narrowly separated; a low chondrophoral ridge wraps around anterior margin of adductor muscle scar; short, linear, anterior lateral extensions of ligament present. Posterior aperture has three to four pairs of short, suprasiphonal papillae, the ventral pair slightly larger. There are about nine small, siphonal papillae around the ventral margin of the aperture. A single unpaired papilla lies dorsal to the aperture.

Distribution. Moreton Bay, Queensland to South Australia.

Habitat. In Moreton Bay, *S. (S.) velesiana* was shallow burrowing in seagrass (*Cymodocea*, *Zostera*, *Halodule* and *Halophila*) covered sands where it co-occurred with other chemosymbiotic bivalves, the lucinids, *Pillucina*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vietnamica Zorina, 1978 and *Anodontia omissa* (Iredale, 1930).

Remarks. Iredale (1931) introduced this species on the grounds that no large *S. australis*-like specimens are found in New South Wales and thus the smaller Sydney species was distinct. He gave no formal description or figure but stated that it differed from *S. terraereginae* in being "...more dilated anteriorly and more closely ribbed posteriorly". Note that Iredale introduced the species as *Solemya* on p. 201, but on p. 202 he named it as the type species of the new genus *Solemyarina*.

Solemya (Solemyarina) terraereginae Iredale, 1929
(Figs 5A–G)

Solemya terraereginae Iredale, 1929: 262, pl. 30, fig. 13.
Solemyarina terraereginae – Iredale, 1939: 233.
Solemya (Solemyarina) velesiana – Lamprell & Healy, 1998: 42, fig. 49 (in our opinion this figured specimen (AMS C 150118) from Bowen, Central Queensland is *S. terraereginae*).

Material Examined. HOLOTYPE. One whole shell, Green I., Queensland (see Iredale 1939: 233) (AMS C 10074). Length 11.1 mm. OTHER MATERIAL. Queensland: Bowen (fig'd specimen in Lamprell & Healy as *S. velesiana*) (AMS C 150118); Innisfail, Kurramine Beach (AMS); Fraser I. (AMS); Swain Reef (AMS); 10-12 fathoms off Michaelmas Cay (AMS); Lizard I., Mangrove Beach (BMNH; AMS); Lady Musgrave I. (AMS C 150115, C 150117); Cooktown, Annan River Mouth (AMS); Great Palm I. (AMS); Torres Strait, S. side of Thursday I. (AMS).

Description. Shell small, length to 8 mm, dorsal and ventral shell margins sub-parallel, periostracum straw-coloured, with faint, evenly spaced rays. Internal ligament (Figs 5 C, E) with dorsal edges of chondrophore parallel and narrowly separated; posterior margin of chondrophore sinuate; anterior end of ligament enlarged into pads and anterior linear lateral extensions present. The aperture (Fig. 5F) has a single dorsal papilla, four pairs of short suprasiphonal papillae, with the largest of these ventral, and 8–9 short, siphonal papillae at the ventral margin.

Distribution. Queensland.

Habitat. At Lizard Island, Queensland, *S. (S.) terraereginae* occurred in lagoon sands (J.T & E.G. pers. observ.) with a sparse covering of the seagrass *Halophila* and in association with the lucinid bivalves *Anodontia ovum* (Reeve, 1850), *Chavania striata* (Tokunaga, 1906) and *Wallucina fijiensis* (Smith, 1885).

Remarks. This species is closely similar to *S. velesiana* but is smaller (length <8 mm), with a paler colour and less prominent radial ribs. The ligament is similar in both species but in *S. terraereginae* the posterior edge of the chondrophore is sinuous rather than straight as in *S. velesiana*. In anatomical characters the gill filaments are much thinner in *S. terraereginae* (9–12 mm compared to 18–20 mm of *S. velesiana*) see also Kreuger & Cavanaugh 1997, fig. 2). The arrangement of papillae around the posterior aperture is similar in both species.

Solemya terraereginae was synonymised with the southern Australian species, *S. australis*, by Lamprell & Healy (1998) and in the Database of Indo-Pacific Marine Molluscs (http://data.acnatsci.org/obis/search.php) but comparison with the type material shows that this is incorrect (compare Figs 3 & 5).

Solemya (s.l.) moretonensis sp. nov.
(Figs 6A–G)

Material Examined. HOLOTYPE. One whole shell, length 5.4 mm, Moreton Bay, north end of Moreton I., Queensland, 26° 56.60' S, 153° 24.25' E, 31 m. (QM-Mo74208); PARATYPES: same locality: one preserved animal (Fig. 6C, BMNH-20060153); one dry shell Fig 6E (QM-Mo74209). F. one animal dried (Fig. 6F, BMNH-20060154); two preserved animals (QM-Mo74210; four dry shells (BMNH-20060155); one preserved animal and three valves (BMNH-20060156).

Description. Shell small, fragile, length to 6.6 mm, shell and periostracum transparent to slightly yellowish. Faint radial ribs visible anteriorly and posteriorly. Ligament with dorsal margins of chondrophore diverging; posterior

◀ FIG. 4. A–K. *Solemya (Solemyarina) velesiana* (Iredale, 1931). A–B, holotype, exterior and interior of right valve (AMS C7476); C–E, exterior and interior of left valve and detail of ligament, Middle Harbour, Port Jackson, Sydney (BMNH 95.3.7.17-19); F, Moreton Bay (BMNH), G, detail of ligament, Moreton Bay (BMNH); H, posterior aperture, Moreton Bay (BMNH); I, papillae at dorsal edge of pedal gape; J, tip of siphonal papilla with ciliary tufts; K, detail of I with single cilia and groups of cilia arising from small pits. Scale bars: A,B,C,D = 5 mm; G = 2 mm; H = 500 µm; I = 250 µm; J = 20 µm; K = 5 µm.

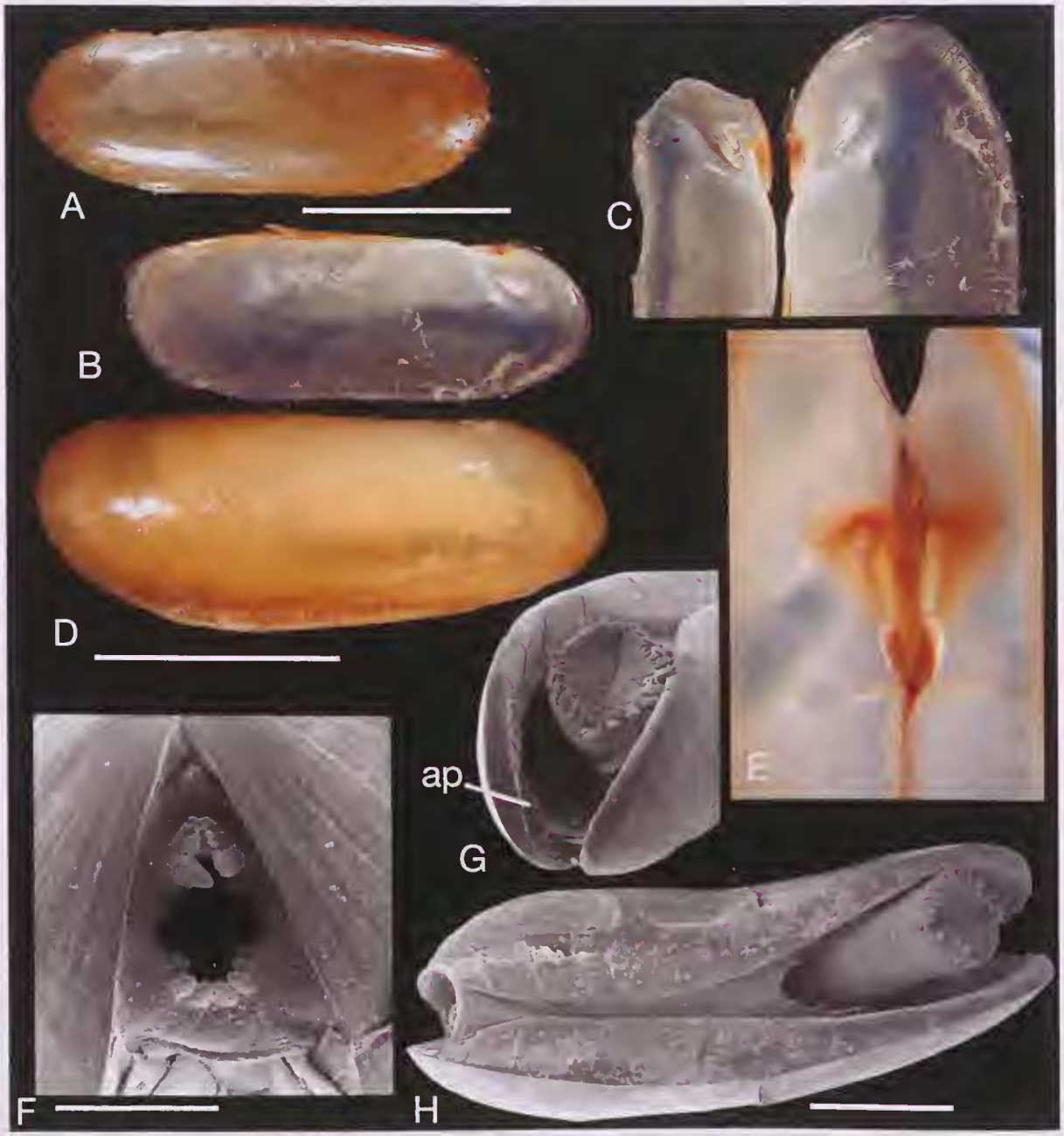

FIG. 5. *Solemya* (*Solemyarina*) *terraereginae* (Iredale, 1929). **A–C**, Holotype, exterior, interior and detail of ligamental area, Green Island, Queensland (AMS C 10074); **D–G**, Mangrove Beach, Lizard Island, Queensland; **D**, left side of preserved animal (BMNH); **E**, internal view of ligamental area; **F**, posterior aperture; **G**, anterior view showing anterior papilla in pedal gape; **H**, ventral view showing pedal gape and mantle fusion. ap = anterior papillae. Scale bars: A,B,C,D = 5 mm; F = 500 µm; G = 2 mm.

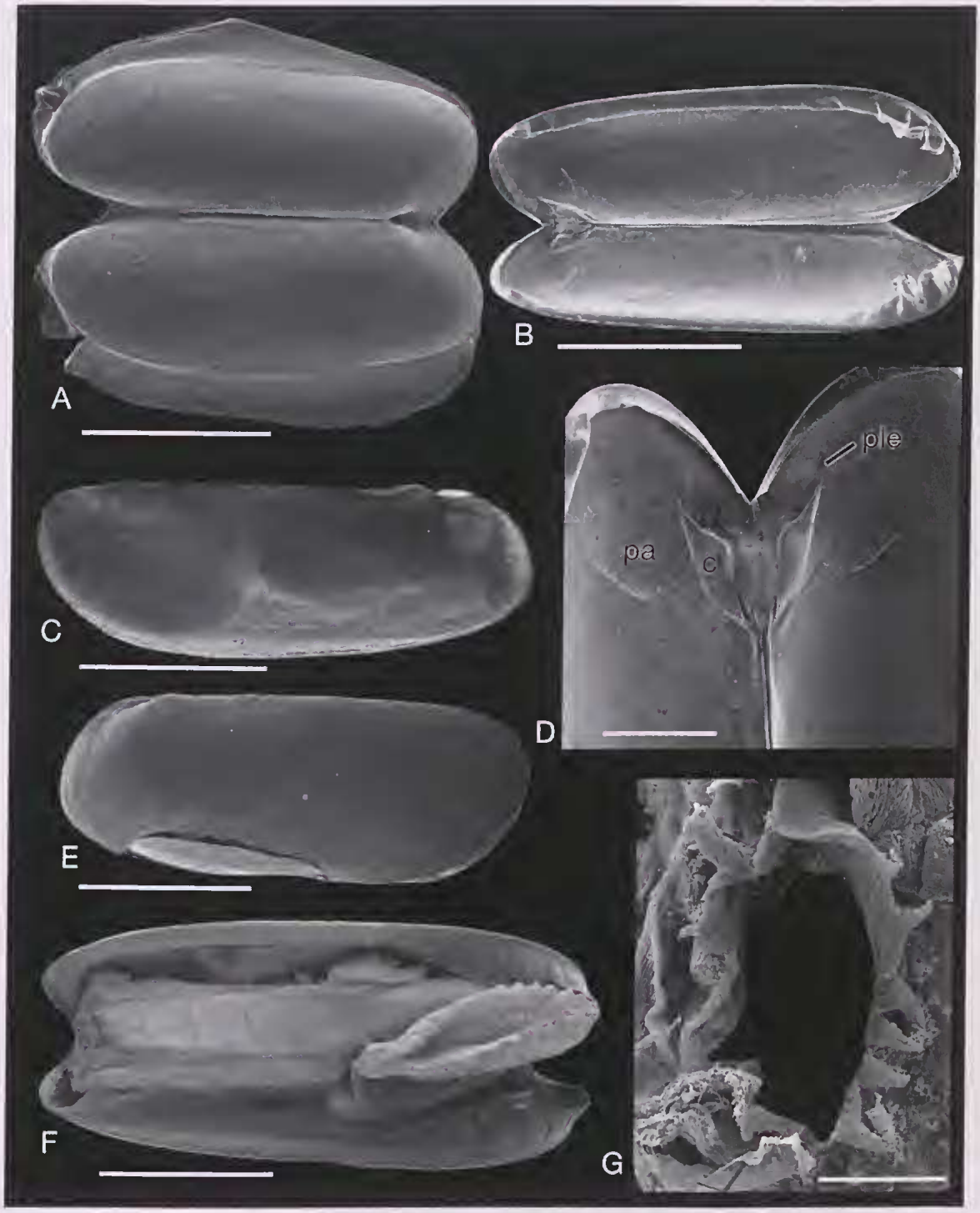

FIG. 6. *Solemya* (s.l.) *moretonensis* sp. nov. **A**, Holotype (QM-Mo74208) exterior of valves; **B**, ventral view of valves; **C**, paratype (BMNH-20060153) lateral view left valve; **D**, holotype detail of ligamental area; **E**, paratype (QM-Mo74209) right side; **F**, paratype (BMNH 20060154) ventral view; **G**, posterior aperture. c = chondrophore; pa = posterior adductor scar; ple = posterior ligament extension. Scale bars: A, B, C, E = 2 mm; D = 500 µm; F = 1 mm; G = 200 µm.

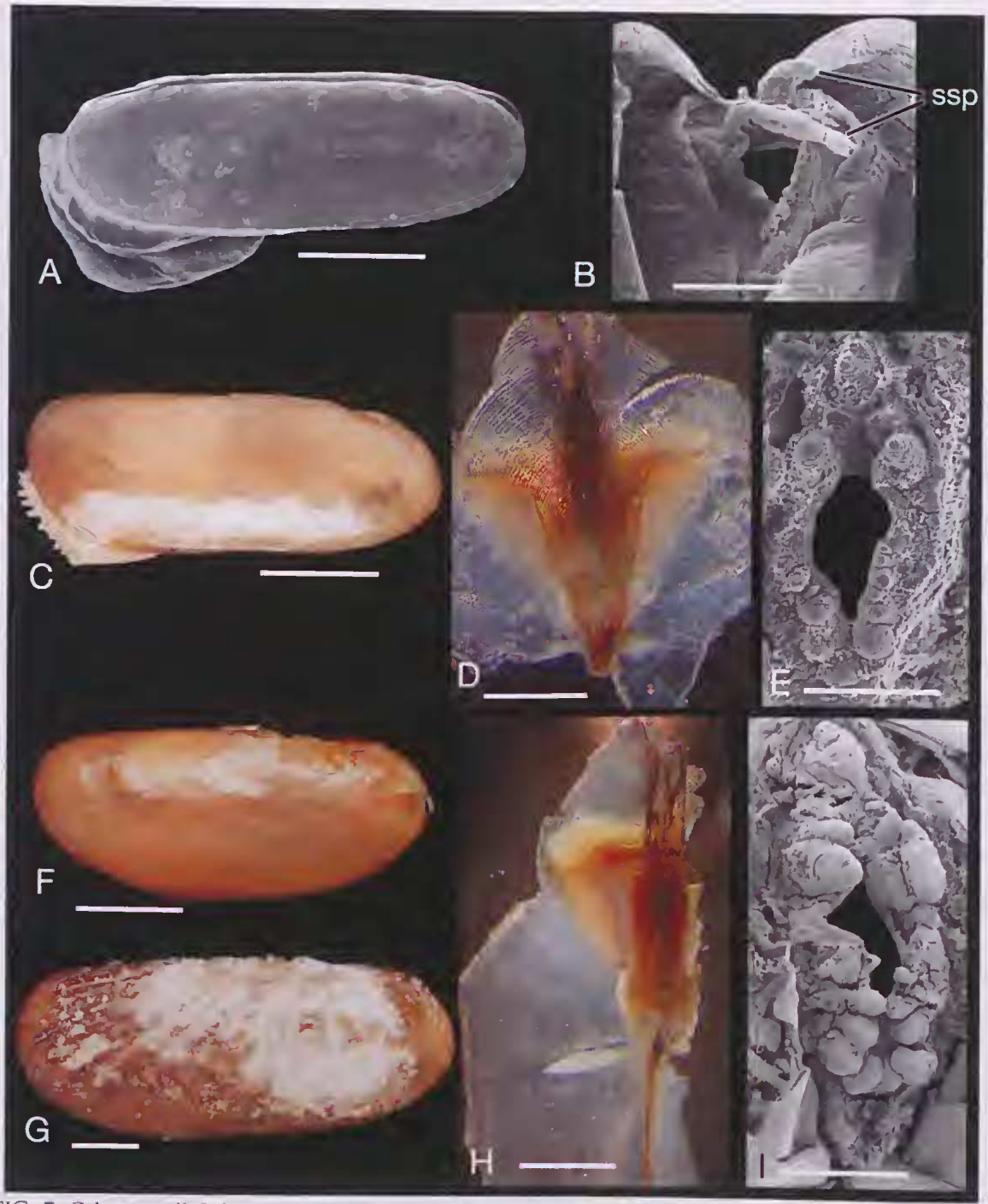

FIG. 7. Other small Solemyidae from Moreton Bay, Victor Harbor, South Australia and Shark Bay, Western Australia. **A–B**, *Solemya* sp. Banana Bank, Moreton Bay, Queensland. **A**, exterior of shell from left side; **B**, posterior aperture; **C-E**, *S.* (*Solemyarina)* species A. Victor Harbour, South Australia; **C**, external of shell left side; **D**, internal ligament; **E**, posterior aperture. **F–I**, *S.* (*Solemyarina*)species B. Little Lagoon, Denham, Shark Bay, Western Australia; **F**, exterior shell; **G**, another specimen corroded by fixative; **H**, ligamental area; **I**, posterior aperture. ssp = suprasiphonal papillae. Scale bars: A, C, F, G = 2 mm; B, E = 500 µm; D, H, I = 1 mm.

dorsal edge of chondrophore projected as a pointed ridge (Fig. 6D). Chondrophoral ridge around the adductor scar slight. Posterior adductor scar does not extend behind chondrophore. Anterior lateral extensions of ligament absent. Posterior margin of outer ligament with small tongue-like extensions (Fig. 6D ple). The posterior aperture (Fig. 6G) is not well preserved but appears to have some suprasiphonal papillae; the most ventral of these is very long. Siphonal papillae probably extend around the apertural margin with likely 12–14 in total.

Remarks. From external characters, this small species might be considered as a juvenile of *S. velesiana*, but the structure of the ligament differs in lacking anterior lateral extensions, the resilium is broad and triangular and the posterior ends of the chondrophore are pointed. Additionally, the siphonal papillae are longer and seem to extend around the aperture rather than grouped ventrally as in *S. velesiana*. The generic placement of this species is uncertain but the ligament, chondrophore and resilium resemble the New Zealand species *S. (Zesolemya) parkinsonii*, although it lacks the anterior, linear, lateral ligament extensions of that species.

Solemya (s.l.) undescribed species
(Figs 7A, B)

Material Examined. A single specimen, shell length 7.3 mm, from mud, Banana Bank, southern Moreton Bay, 26°56.6'S, 153°24.25' E (BMNH-20060159)

Remarks. In addition to *S. velesiana* and *S. moretonenis* from Moreton Bay, we have a single specimen of a third species. Although similar to *S. velesiana* in external shell characters, the posterior aperture differs in having a pair of long suprasiphonal papillae (Fig 7B) and short siphonal papillae. The internal ligament also lacks anterior lateral extensions. The characters of the posterior aperture with the long pair of suprasiphonal papillae are more similar to *Solemya* and *Petrasma* species (see Fig 2 A,B) than to *Solemyarina*. Further sampling of solemyids in Moreton Bay should reveal more details of this species

In addition to the species described above we recognise two other taxa based on molecular data and some morphological characters but we have insufficient well- preserved material of these for formal descriptions in this paper. Specimens were cracked and fixed in the field in 100 % ethanol for molecular analysis and, as a result, some of the diagnostic morphology such as the posterior apertures are poorly preserved. On the basis of ligament characters we would include them within the concept of *Solemyarina*; *Solemyarina* sp. A from Victor Harbor, South Australia and *Solemyarina* sp. B from Shark Bay, Western Australia.

Solemya (Solemyarina) species A
(Figs 7C, D, E)

Material Examined. Eight individuals — one complete animal and remainder with shells cracked or dissected, Anchorage Bay, Victor Harbor, South Australia (BMNH-20060150).

Description. Shell small, length to 7.3 mm, thin shelled, pale brown to fawn with faint white rays, to anterior and posterior. Chondrophore margins widely spaced with a triangular resilium. The posterior margin of chondrophore is more or less straight. Chondrophoral buttress slight. Anterior lateral extensions of ligament are short and narrow. On the only specimen where the posterior aperture was visible it is similar to *S. velesiana* but there appear to be more siphonal papillae (Fig. 7E).

Habitat. Collected from thin, muddy sand on intertidal rock platform with *Heterozostera*, *Posidonia australis* and *Amphibolis*. The solemyids occurred in association with the lucinid bivalves, *Epicodakia tatei* (Angas, 1879), *Notomyrtea ada* (Adams & Angas, 1863) and *Anodontia perplexa* (Cotton & Godfrey,1938).

Remarks. This species occurs within the geographical range of *S. (Austrosolemya) australis* but differs in size, colour and form of ligament.

Molecular evidence from sequences of the cytochrome B gene (Table 2) indicates that this species is distinct from both *S. (Solemyarina) velesiana* from Moreton Bay and *S. (S.)* sp. B from Shark Bay by 17% & 19% (Kimura distance) respectively.

Solemya (Solemyarina) species B
(Figs 7F–I)

Material Examined. Three individuals (two dissected), lengths 11.9–12.4 mm, Little Lagoon, Denham, Shark Bay, Western Australia, mud and

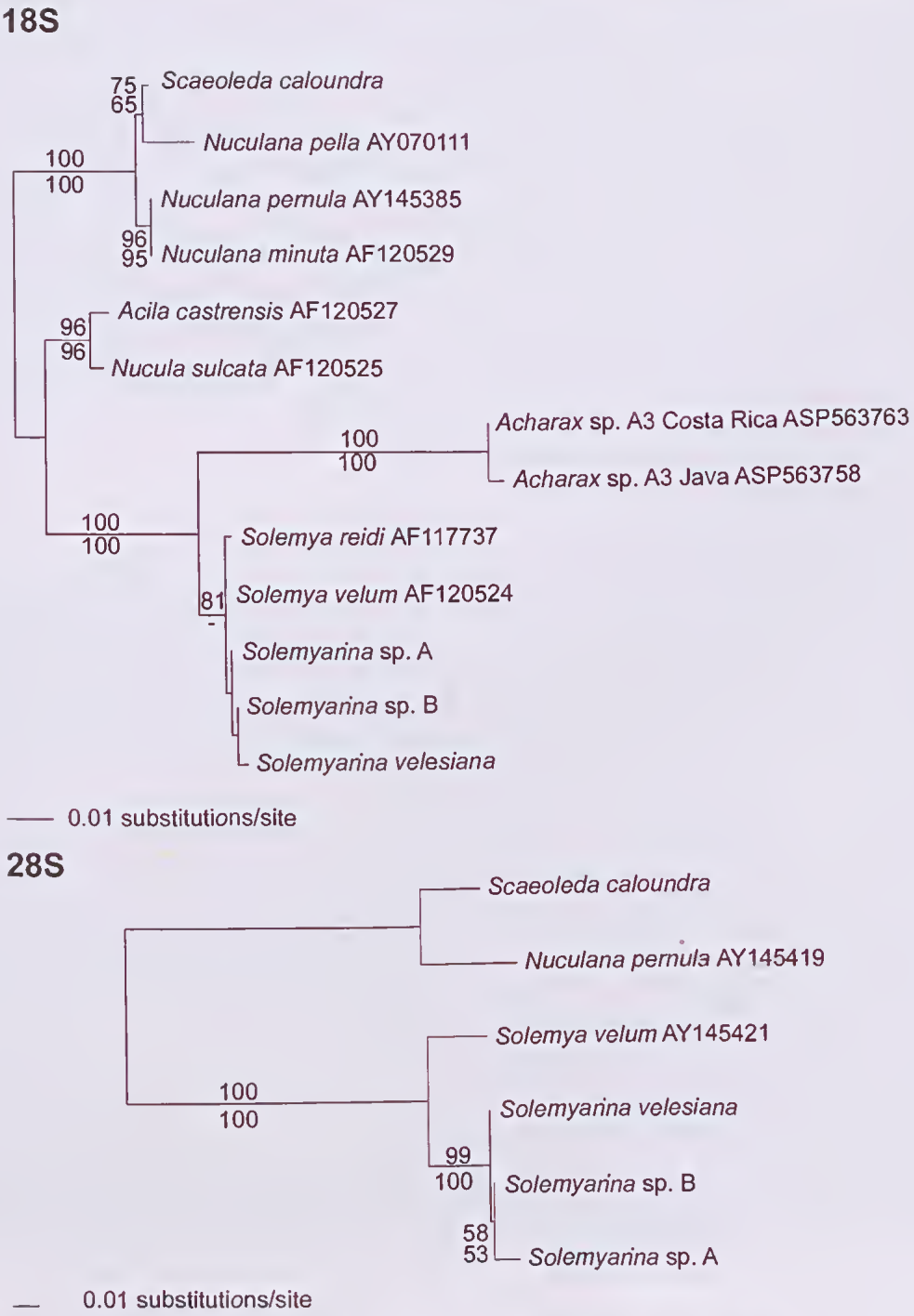

FIG. 8. Molecular phylogenies for single gene analyses of 18S rRNA and 28S rRNA genes produced by maximum likelihood analyses. *Scaeoleda* and *Nuculana* (Nuculanidae) were drawn as the outgroup. Nodal support above branches is based on maximum likelihood (ML) bootstrap values and below branches, neighbour joining using ML distances.

Table 1. List of species used in the molecular analysis with voucher and GenBank accession numbers. Full details are given for the new analyses reported in this study.

Species	Location	Voucher reg no	18S	28S	Cyt B
Nuculidae					
Nucula sulcata Bronn, 1831			AF120525		
Acila castrensis (Hinds, 1843)			AF120527		
Nuculanidae					
Nuculana minuta (Müller, 1776)			AF120529		
Nuculana pella (Linnaeus, 1767)			AY070111		
Nuculana pernula (Müller, 1779)			AY145385	AY145421	
Scaeloleda calaundra (Iredale, 1929)	Moreton Bay, Qld	BMNH 20060149	AM293663	AM293664	
Solemyidae					
Acharax sp. Costa Rica			ASP563763		
Acharax sp. Java			ASP563758		
Solemya reidi Bernard, 1980			AF117737		
Solemya velum Say, 1822			AF120524	AY145421	
Solemyarina velesiana (Iredale, 1931)	Moreton Bay, Qld	BMNH 20060151	AM293669	AM293668	AM293670
Solemyarina sp. A	Victor Harbor, SA	BMNH 20060150	AM293666	AM293667	AM293665
Solemyarina sp. B	Denham, Shark Bay, WA	BMNH 20060152	AM293672	AM293673	AM293671

Table 2. Kimura 2-parameter distance matrix for cytochrome B sequences.

	1	2
Solemyarina A (Victor Harbor)	-	
Solemyarina B (Shark Bay)	0.196	
Solemyarina velesiana (Moreton Bay)	0.174	0.097

dead algae in mangrove channel (BMNH-20060152 molecular voucher; BMNH-20060160).

Description. Small, length to 12.4 mm, yellow brown with slightly raised pale rays. Ligament with chondrophore margins not widely separated, heart-shaped anterior area with narrow anterior extensions of the ligament at 90° to shell margin. Posterior margin of chondrophore sinuate. Posterior aperture with prominent suprasiphonal and large siphonal papillae around the ventral margin of the aperture.

Remarks. Characters of the ligament, chondrophore shape and anterior lateral extensions are most similar to *S. (S.) terraereginae* from Queensland, but the posterior aperture of the Shark Bay species has larger siphonal and suprasiphonal papillae. Molecular evidence from cytochrome B sequences shows that this species is separated from *S. (S.) velesiana* from Moreton Bay by 9.8% (Kimura distance).

MOLECULAR ANALYSIS

Sequences from 18S rRNA and 28S rRNA and cytochrome B genes were obtained from three species: *S. (Solemyarina) velesiana* from Moreton

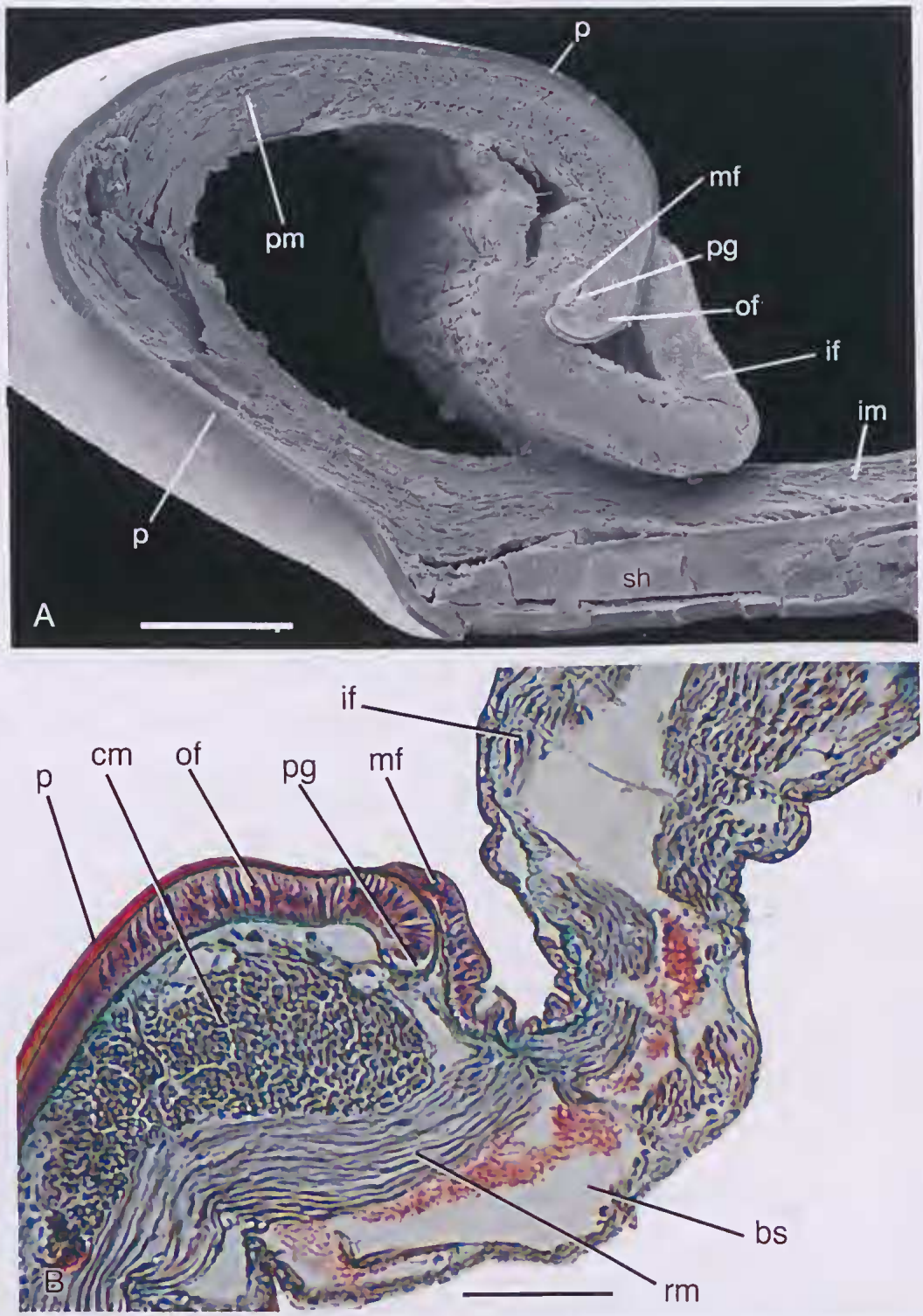

FIG. 9. Mantle margin of *Solemya (Solemyarina) velesiana*. **A**, cut shell edge and mantle margin; **B**, thin section of mantle edge to show mantle folds and periostracal groove. Scale bars: A = 200 μm; B =100 μm. bs = blood space; cm = circular muscle; if = inner mantle fold; im = inner mantle; mf = middle mantle fold; of = outer mantle fold; p = periostracum; pg = periostracal groove; pm = pallial muscles; rm = radial muscles; sh = shell.

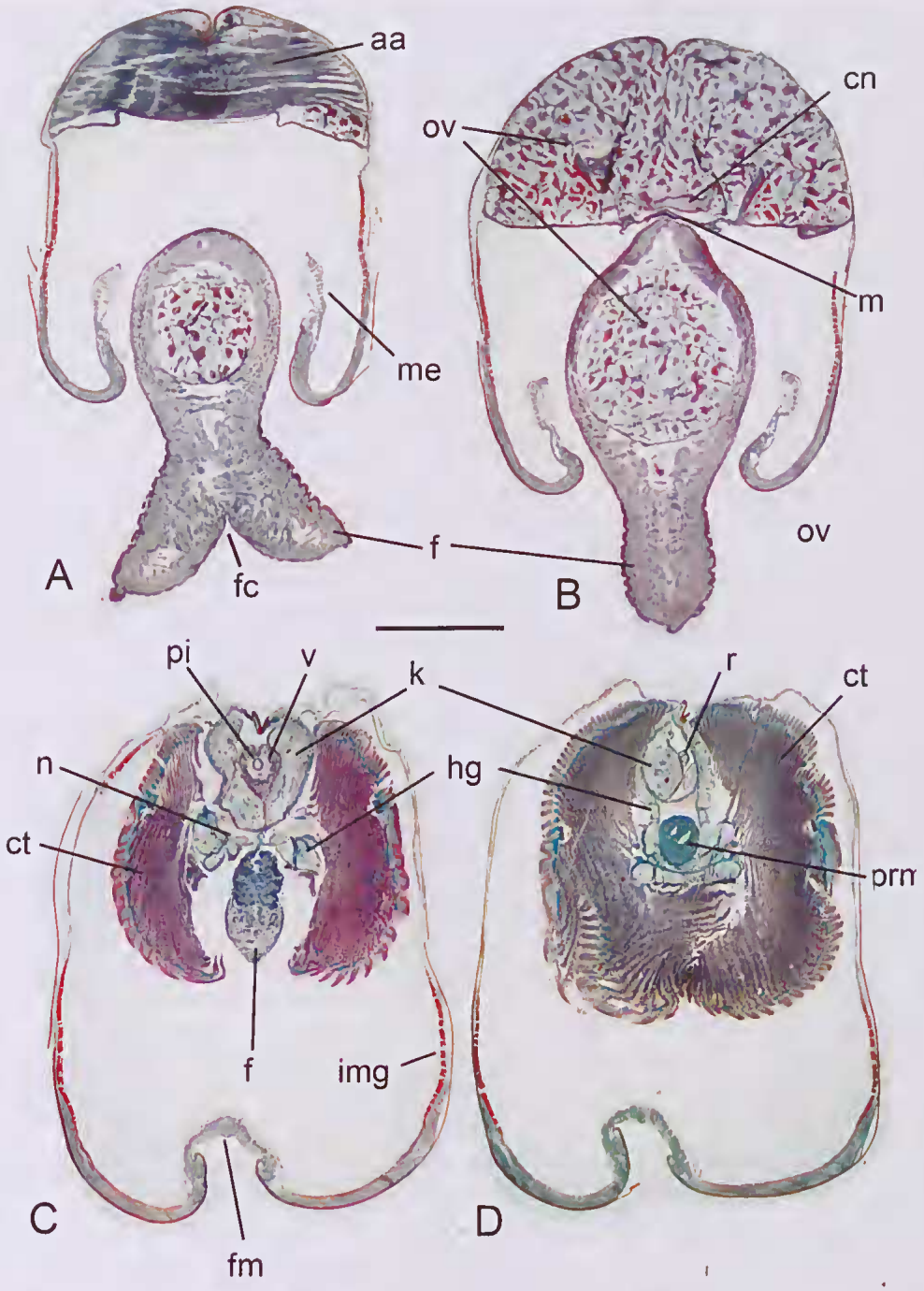

FIG. 10. **A–D**. four sections from anterior to posterior through body of *Solemya (Solemyarina) velesiana* from Moreton Bay. **A**, anterior section through anterior adductor muscle and foot; **B**, section through mouth with ovary and foot; **C**, section around midline through ventricle and ctenidia; **D**, posterior section through ctenidia and hypobranchial gland. Scale bar = 1.0 mm. aa = anterior adductor muscle; cn = circum-oral nerve; ct = ctenidium; f = foot; fc = foot cleft; fm = fused mantle; hg = hypobranchial gland; k = kidney; l = ligament; m= mouth; me = mantle edge; img = inner mantle gland; n = nerve; ov = ovary; pe = periostracum; pi = posterior intestine; prm = pedal retractor muscle; r = rectum, v = ventricle.

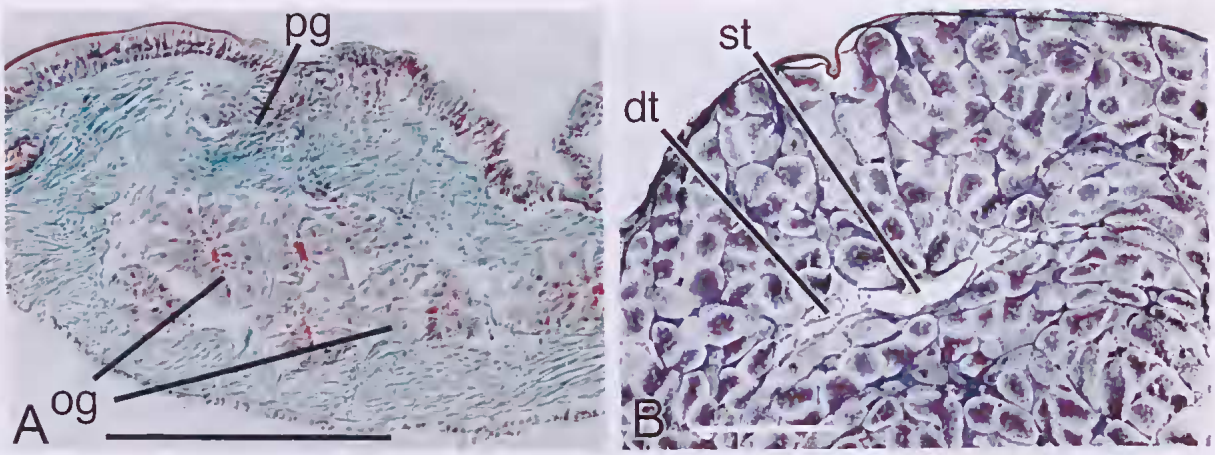

FIG. 11. *Solemya (Solemyarina) velesiana*. A, section of anterior mantle with tubular "oil glands"; B, section through ovary and stomach. Scale bars: A= 200 µm; B = 500 µm. dt digestive tubules; og = oil glands; pg = periostracal groove; st = stomach.

Bay, *S.* (*Solemyarina*) sp. A from Victor Harbor and *S.* (*Solemyarina*) sp. B from Shark Bay. Unfortunately, we failed to extract and amplify DNA from the *S. (Solemyarina) terraereginae* samples from Lizard Island and no suitably preserved specimens of *S. (Austrosolemya) australis and S. moretonensis* were available for analysis. Additionally, sequences of other Solemyidae obtained from GenBank were included in the analysis - two species of *Acharax* (Neulinger *et al*, 2006), *Solemya (Petrasma) velum* and *S. reidi*. The sequence data for *Solemya togata* lodged in GenBank has anomalous features and was not used in our analysis. These solemyids were compared with other protobranch bivalves as outgroups, namely four species of Nuculanidae and two species of Nuculidae. All new sequences have been deposited in GenBank (Table 1).

A single maximum likelihood tree was obtained for 18S rRNA (-ln L = 2094.184) and for 28S rRNA (-ln L = 3465.939) (Fig. 8). Sequences for more taxa were available for 18S rRNA so the two trees are not directly comparable, although there are no significant incongruencies. In the 18S tree (Fig 8A) the Solemyidae, including *Acharax*, form a well-supported clade, with *Acharax* forming a sister clade to the shallow water *Solemya* species. The results also indicate Solemyidae are more closely related to Nuculidae than Nuculanidae.

In the 28S rRNA tree the three Australian species form a well-supported clade distinct from *Solemya (Petrasma) velum* from eastern America but this is less well supported in the 18S tree. Relationships between Australian species are poorly supported. Sequences from the cytochrome B gene gave better resolution of relationships amongst these species. Distance estimates (Table 2) based on a single sequence for each species (Kimura 2-parameter (Kimura 1980)) suggested that the *S.* (*Solemyarina*) sp. B from Shark Bay is more closely related to *S. Solemyarina velesiana* from Moreton Bay (9.8%) than either are to *S.* (*Solemyarina*) sp. A from Victor Harbor (Sol. A: Sol. veles =17.5%; Sol. A: Sol. B =19.7%). These distances are well above the cut-off values normally indicative of separate species.

MORPHOLOGY OF *S.* (*SOLEMYARINA*) *VELESIANA*

Very few solemyid species, particularly those from the Indo-West Pacific, have been documented in any detail and in this section we describe and illustrate some major features of the anatomy of *Solemya (Solemyarina) velesiana* from Moreton Bay. We also studied the anatomy of *S.* (*S.*) *terraereginae* that is similar in most respects, except for the thickness of the ctenidial lamellae and bacteriocytes.

MANTLE FUSION AND APERTURES

The mantle is fused along the entire posterior half of the ventral margin with a large anterior pedal gape and a single aperture to the posterior. The ventral edges of the mantle surrounding the pedal gape bear a few short

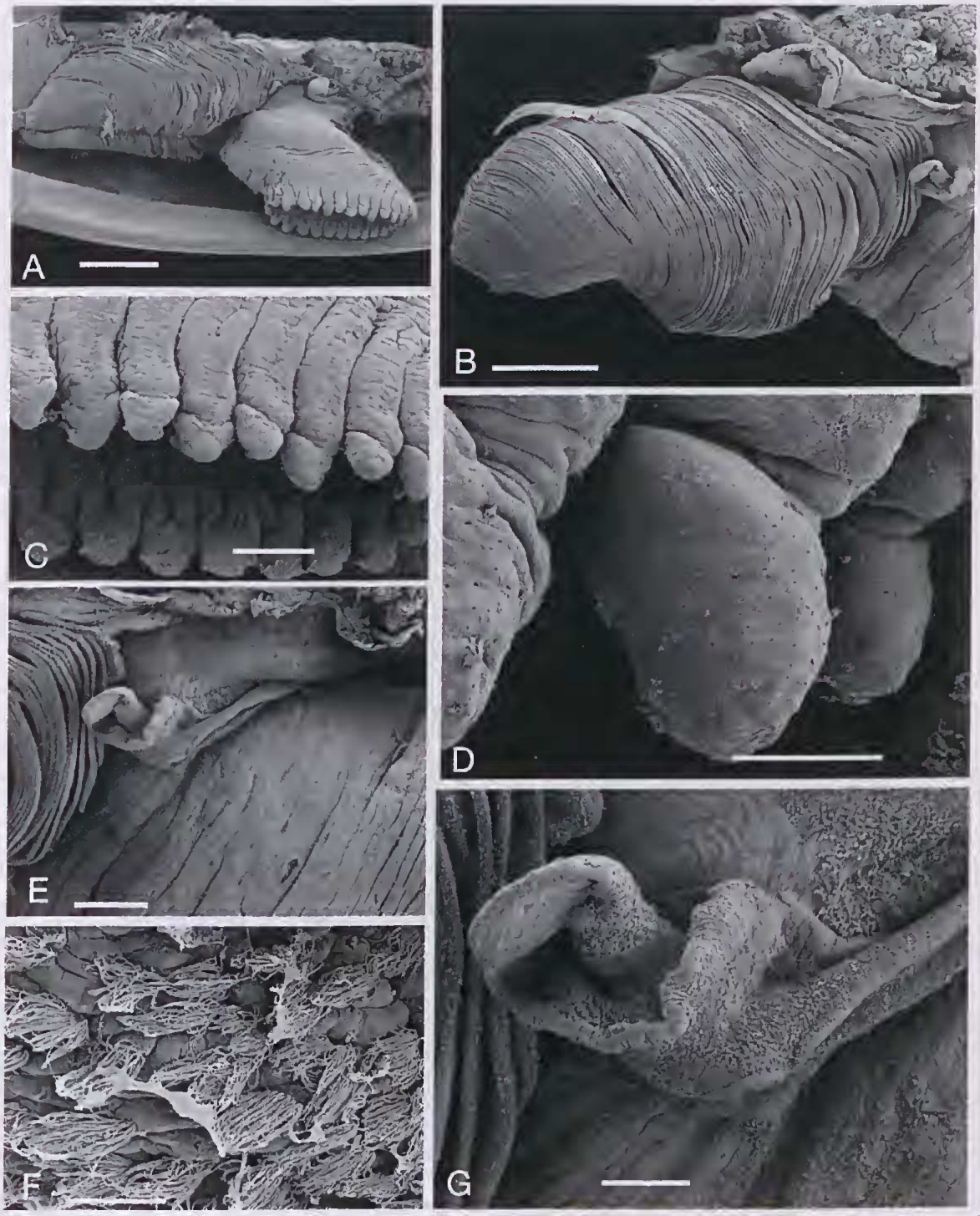

FIG. 12. *Solemya (Solemyarina) velesiana* Moreton Bay, details of anatomy. A, right valve and mantle removed to show foot, ctenidium and palp proboscis, scale bar = 1 mm; B, right ctenidium, scale bar = 1 mm; C, detail of foot showing papillate fringe, scale bar = 200 μm; D, detail of tip of foot papilla, note pores, scale bar = 50 μm; E, palp proboscis and groove leading to mouth, scale bar = 500 μm; F, ciliary tufts on surface of palp, scale bar = 20 μm; G, detail of distal end of palp with surface of ciliary tufts, scale bar = 200 μm.

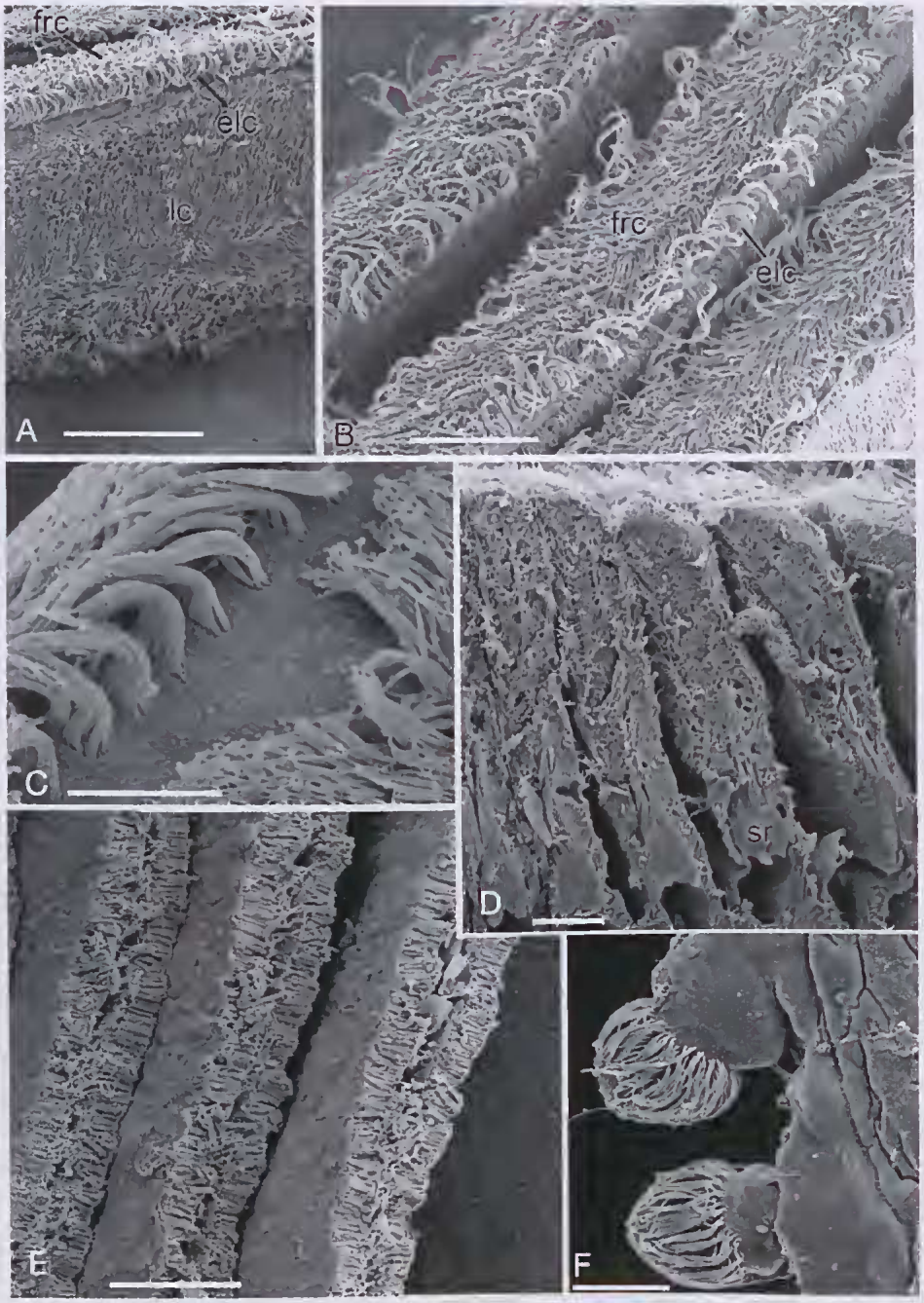

FIG. 13. A–F. *Solemya (Solemyarina) velesiana* Moreton Bay, details of ctenidia. A, lateral view of outer portion of gill lamella with band of lateral cilia and eulatero-frontal and frontal cilia. scale bar = 50 µm; B, outer edge of lamella showing eulaterofrontal and frontal cilia, scale bar = 20 µm. C, bases of eulatero-frontal cilia, scale bar = 5 µm; D, transverse sections through distal ends of several lamellae showing supporting rods, scale bar = 20 µm; E, sections through three adjacent lamellae packed with bacteria, scale bar = 20 µm; F, ciliated tufts (ciliated knobs of Yonge 1939) from abfrontal edge of gill lamellae, scale bar =10 µm. frc = frontal cilia, elc = eulatero-frontal cilia; lc = lateral cilia; sr = supporting rod.

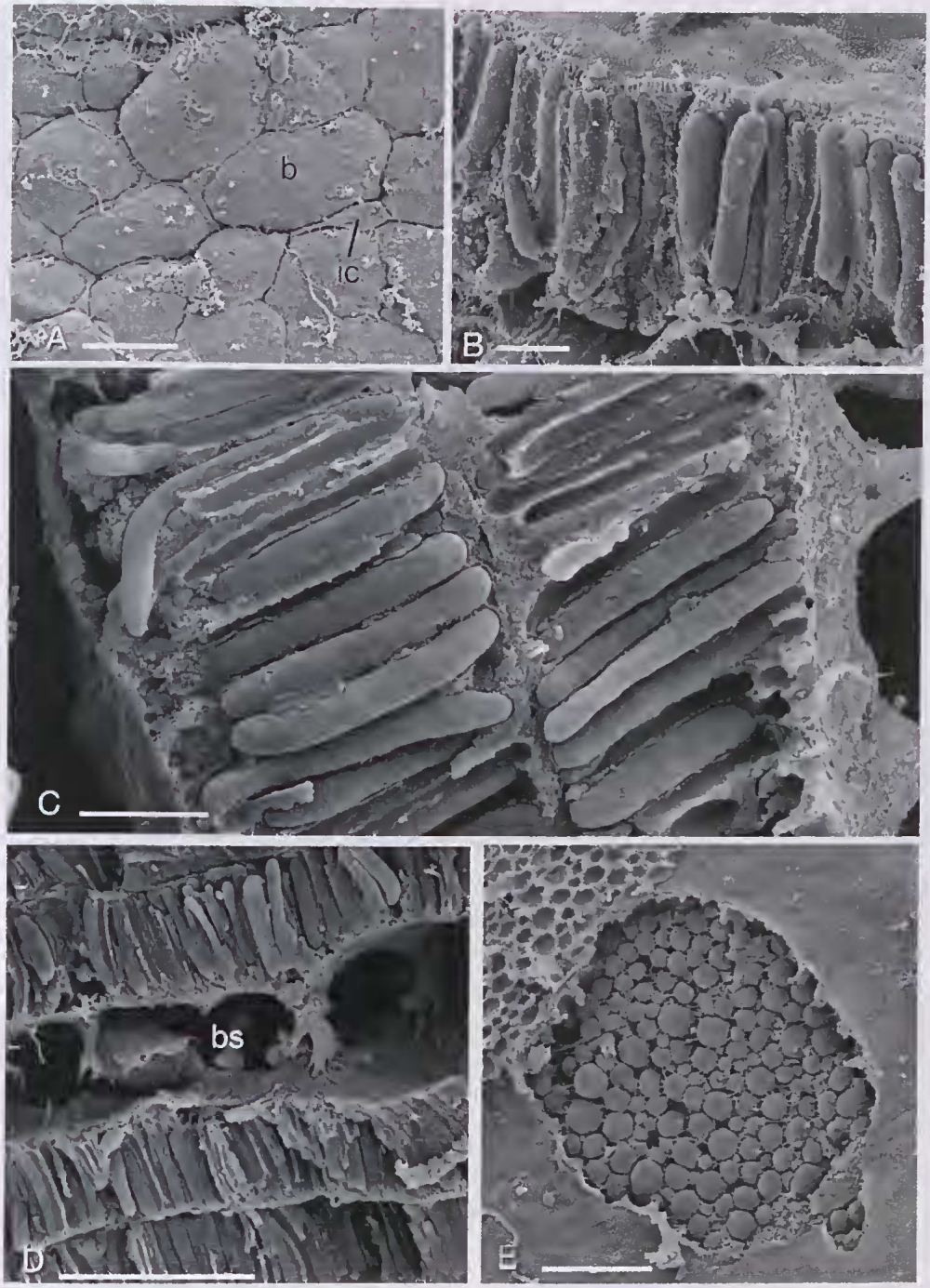

FIG. 14. *Solemya* (*Solemyarina*) *velesiana* Moreton Bay, details of bacteriocytes. A, surface of gill lamella showing outer surfaces of bacteriocytes and intercalary cells, scale bar = 10 µm; B, section of lamella with bacteria aligned vertically in bacteriocytes beneath the microvillli, scale bar = 2 µm; C, two adjacent gill lamellae with aligned bacteria, scale bar = 2 µm; D, central blood space between sheets of bacteriocytes, scale bar = 10 µm; E, surface of bacteriocyte peeled back to show tips of bacteria packed within, scale bar = 5 µm. b = bacteriocyte; bs = blood space; ic = intercalary cell.

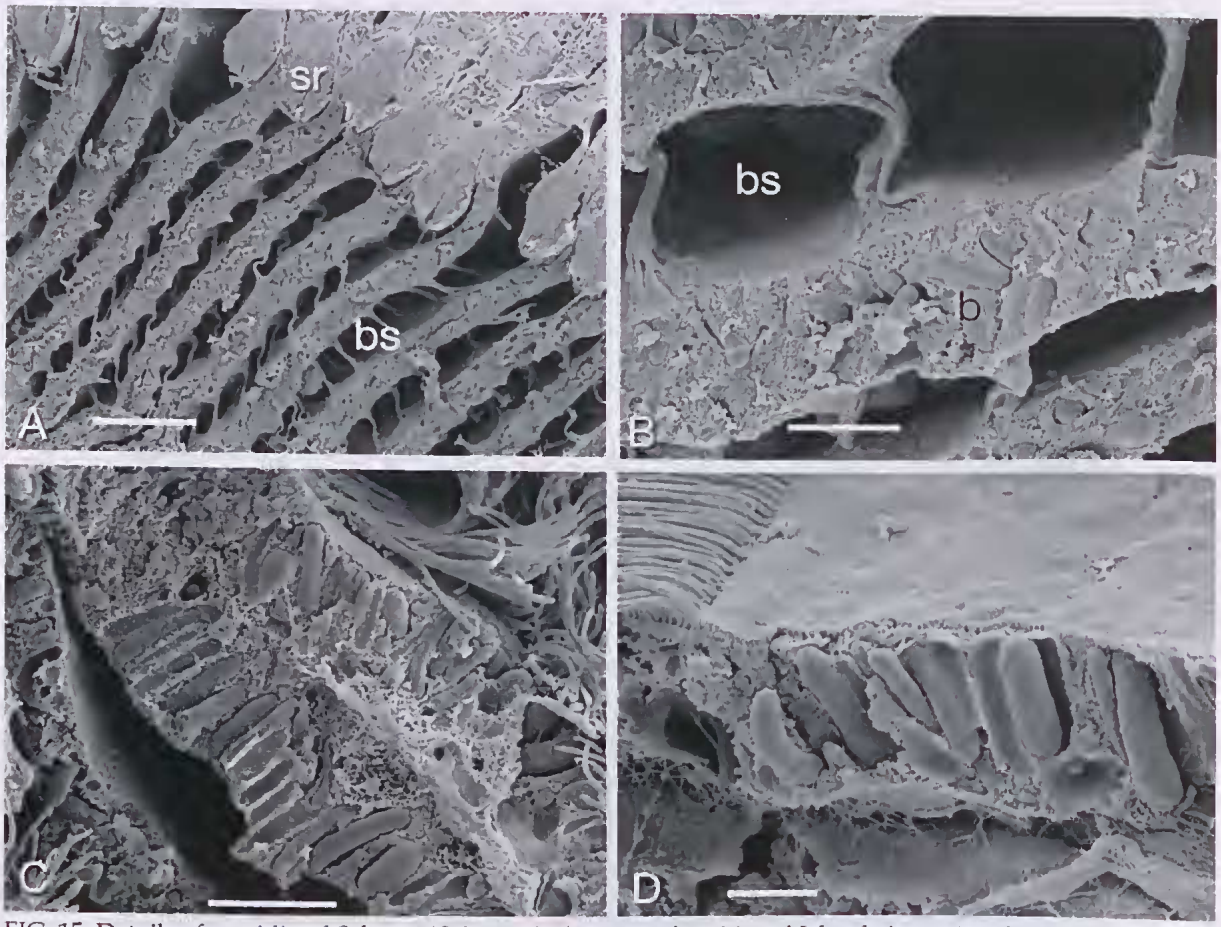

FIG. 15. Details of ctenidia of *Solemya (Solemyarina) terraereginae* Lizard Island. **A**, section through several gill lamellae scale bar = 20 μm; **B**, detail of lamellae and blood space, scale bar = 5 μm; **C**, first bacteriocytes in gill lamella, scale bar = 5 μm; **D**, detail of bacteria beneath microvilli, scale bar =2 μm; b= bacteria; bs = blood space; sr supporting rods.

papillae, with larger, stubby papillae at the antero-dorsal margins of the pedal gape. The posterior aperture possesses two sets of papillae; there are nine to ten siphonal papillae around the ventral margin decreasing in size laterally. On each side of the dorsal edge of the aperture there are four suprasiphonal papillae and above these a single dorsal papilla (Fig. 4H). The siphonal papillae have two types of putative sensory structures at their tips; either with single long cilia, or pits with groups of ca 20 short, stiff cilia (Fig. 4 I, J).

The mantle margin is thick and muscular with three folds; a large outer fold, a small, thin middle fold and a large and muscular inner fold (Fig. 9). Mantle fusion along the ventral margin of *Solemya* involves only the inner fold (Fig. 10). One of the more remarkable features of all solemyids is the broad, marginal periostracal fringe. The periostracum arises in a narrow groove between the outer and middle folds, with the outer surface of the middle fold tightly appressed to it (Fig. 9B). The periostracum gradually thickens (to ca 25 μm) around the outer surface of the outer mantle fold and three distinct layers are visible from differential staining. A complex system of radial muscles ("orbicular" muscles of Beedham & Owen, 1965) occupies the periostracal fringe (Fig. 9A). Some of these extend from the mantle within the calcified shell into the periostracal fringe, others cross-connect the periostracum within the fringe, while others extend into the folds of the mantle margin. The inner mantle

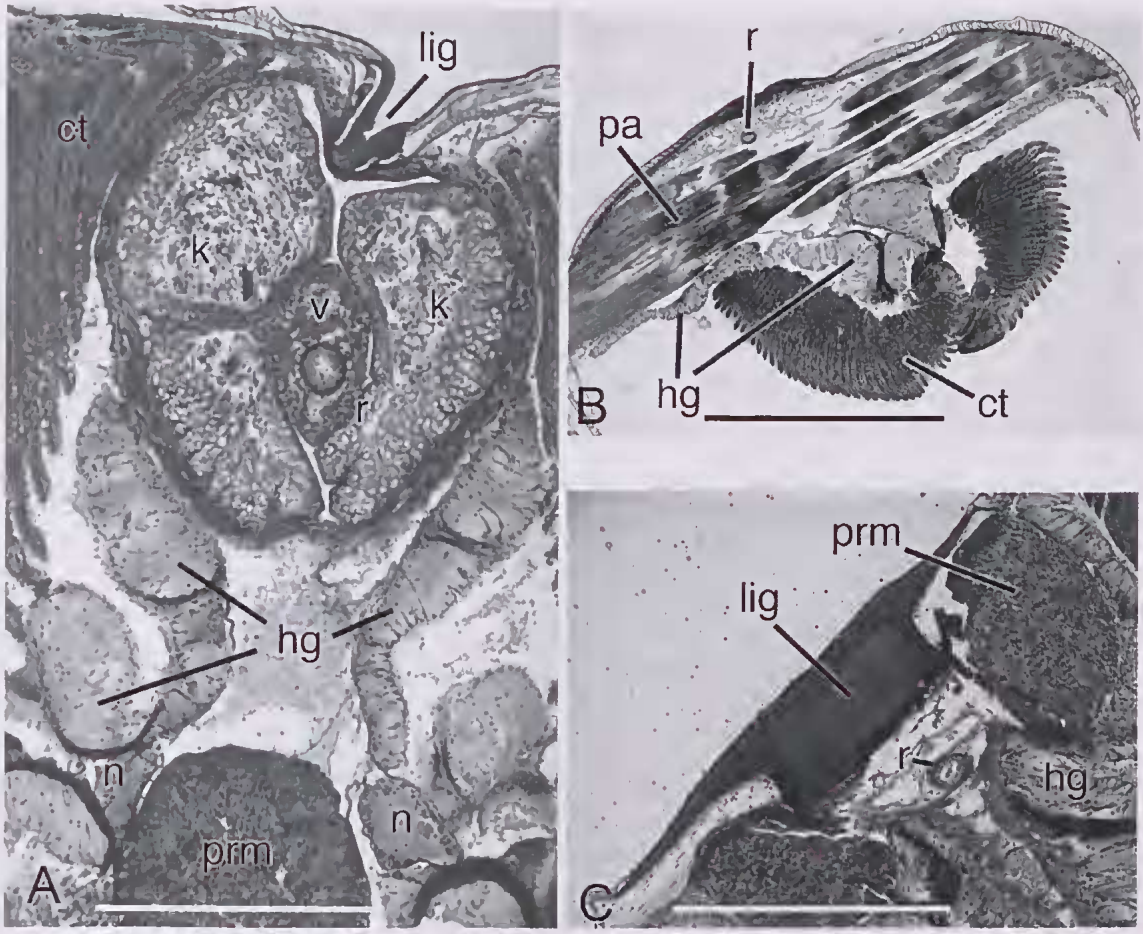

FIG. 16. Histological sections through *Solemya (Solemyarina) velesiana*, Moreton Bay. A, section through posterior of *S. velesiana* showing extensive hypobranchial gland and ventricle; B, section through posterior showing hypobranchial gland on inner mantle; C, section through posterior ligament resilifer. Scale bars: A,B,C = 500 µm. ct = ctenidia; hg = hypobranchial gland k = kidney; lig = ligament; n = nerve; pe = pericardium; prm = pedal retractor muscle; r = rectum; v= ventricle.

fold is also highly muscular, with bundles of circum-pallial muscles as well as radial and transverse muscles. Calcification on the inner surface of the periostracum commences around 2 mm from the mantle margin and comprises an outer layer of irregular "prisms" with thick organic boundaries between the prisms and a thin, inner layer of homogeneous/platy crystals.

The anterior and posterior mantle margins have distinctive tubular glands, the so-called oil glands of Beedham & Owen (1965). These glands, located in the proximal part of the inner mantle, open into the groove between the inner and middle mantle folds (Fig. 11A). It has been suggested (Yonge, 1939; Beedham & Owen, 1965) that the glands secrete a lipo-protein responsible for the water-repellant properties of the periostracum. Away from the margins, the mantle is very thin, with a low, cuboid, outer epithelium but ventrally, the inner epithelium is glandular with tall glandular cells staining orange-red. This glandular area was called the anterior pallial organ by Stempell (1899) but not mentioned by Yonge (1939) or Beedham & Owen (1965). The function of this gland is uninvestigated.

FOOT

S. (Solemyarina) velesiana has a large foot with a deep central cleft, and is highly extensible, as in most solemyids. The foot is fringed with around 28 papillate projections with differentiated tips (Fig. 12A, C). Numerous small

pores (1–2 μm diameter) open to the surface of the papillae (Fig. 12D). In section, the foot is highly muscular with a small, narrow pedal gland opening into the deep cleft (Fig. 10A). Reid (1980) reported a large spherical mucus gland in the foot of *S. reidi*, but this was not located in our thin sections.

CTENIDIA

The ctenidia are large, brown, bipectinate and occupy most of the posterior half of mantle cavity (Fig. 12A, B). They are composed of around 170–180 crescentic lamellae about 20 μm in width. The distal edge of each leaflet is ciliated (Figs 13A, B, D), with a central tract of frontal cilia, bounded on each side by eulatero-frontal cirri made up of 10 pairs of cilia in two parallel rows (Fig. 13C). A broad band (ca 75 μm wide) of lateral cilia occupies the outer part of the lateral face of each lamella. The rest of each lamella is an unciliated, smooth, microvillii-covered surface. Along the proximal edge of the lamellae are a series of small projections bearing shaving-brush-like ciliary tufts set on short projections (ciliated knobs of Yonge, 1939) about 15 μm in diameter (Fig. 13F). Internally, the ctenidial lamellae comprise the distal ciliated section (120 μm in length) supported by a tapering, double chitinous rod (ca 12 μm in width) (Fig. 13D). At, and proximal to the rod, the ctenidial epithelium changes from cilia-bearing cells (ciliated zone) to the bacteriocyte zone (Fig. 13E) that occupies most of the length of the lamellae. Within the bacteriocyte zone, the lamellae comprise thin sheets of cells (8–10 μm wide) separated by central blood space (Fig. 14D). The epithelial cells are packed with elongate, rod-shaped bacteria (ca 6–7 μm in length, and 1 μm in width) oriented with their long axes normal to the lamellar surface and occupying most of the cell space (Figs 14B, C, E). Surface views of the lamellae (Fig. 14A) show the bacteriocytes to be around 10–20 μm in diameter.

By comparison, the ctenidial lamellae of *S. (Solemyarina) terraereginae* from Lizard Island are thinner (5–7 μm compared with 8–10 μm) and less tightly packed together than *S. (S.) velesiana*. The bacteriocytes (Figs 15) contain smaller, shorter bacteria (2–5 μm long compared with 6–7 μm) that are less densely packed and vary in shape (pleomorphic) from narrow to subspherical (Fig. 15 B-D). A similar morphology for the bacteriocytes of *S. (S.) terraereginae* was recorded from TEM observations by Kreuger & Cavanaugh (1997).

PALPS AND ALIMENTARY TRACT

On either side of the foot are structures that have been interpreted as homologous with, although much shorter than, the palp proboscides of Nuculoidea (Waller, 1998). These are twisted, flap-like structures with cupped distal terminations that lie laterally across the foot with, proximately, a ciliated groove leading to the mouth (Fig 12, E, G). All surfaces of the distal portions of these flaps are covered in ciliary tufts (Fig 12F). We did not observe any structure on the foot similar to the pouch-shaped, ciliated organ described by Reid, 1980 for *S. reidi*.

The mouth is small, with a narrow oesophagus leading to the very small stomach, with the digestive diverticula comprising just few short acini (Fig. 11B). The mid gut is thin and straight, leading to a narrow rectum that passes through the ventricle (Fig. 15), then dorsally to the posterior adductor and terminates at the posterior mantle aperture.

HYPOBRANCHIAL GLAND.

A hypobranchial gland occupies the posterior end of mantle cavity covering the outer surface of the visceral mass and extending ventrally to cover both dorsal and ventral surfaces of the ctenidial axes (Fig. 15A). Dorsal extensions of the glands line the dorsal inner mantle (Fig. 15B). A similar, extensive, hypobranchial gland has been recorded in *Solemya togata* (Pelseneer 1891; Stempell 1899) and *S. parkinsonii* (Morton 1977). In section, the gland comprises large mucous cells separated by narrow, ciliated cells similar to those described for *Solemya parkinsonii* (Morton 1977).

DISCUSSION

Previously, only three species of Solemyidae have been recorded from around Australia, the most well known being the large, southern species *S. australis*. Our recognition of four solemyids from Queensland and other putative species from limited sampling in South and Western Australia suggests that the diversity of

the family in Australia is underestimated, with small species having being largely ignored. Furthermore, amongst the described species there has been considerable nomenclatural confusion both at specific and supraspecific levels (e.g. Lamprell & Healy 1998). One of the problems in solemyid systematics is that shell characters are enigmatic and difficult to assess, for they lack features such shell sculpture and hinge teeth and are all uniformly covered by a distinctive, thick, shiny periostracum. Unraveling of solemyid systematics would be a suitable case for molecular analysis but there are few available sequences from elsewhere lodged in GenBank and our sampling from Australia is very limited. Preliminary molecular results, combined with observations on morphological characters of the ligament and chondrophore and form of the posterior aperture and arrangement of surrounding papillae, support our discrimination of species. Further sampling around Australia is needed to establish the geographic ranges of the species and also to provide additional material for full formal descriptions of the unnamed small species from South and Western Australia. In the process of trying to place the Eastern Australia solemyids into a broader context we undertook a review of ligament and apertural characters of the type species of the recognised genera of Solemyidae, having realised that these are also often misunderstood and applied incorrectly. A particular example is the frequent use of the ligament characters of *Solemya* (*Austrosolemya*) *australis* as the type species of *Solemya* instead of, correctly, *Solemya togata*. Elaborating from Dall (1908a, b), characters of the ligament suggest a number of distinct groups of solemyids that can be tested as more molecular data becomes available.

Of the bivalve families possessing symbiosis with sulphide-oxidising bacteria, the Solemyidae and Lucinidae are the only ones with species commonly inhabiting intertidal and shallow waters, where they live within the sediment at the boundary between oxidised and anoxic zones (Stewart *et al.* 2005; Stewart & Cavanaugh 2006). In both families, the symbiosis seems to be obligate, with some solemyids dependent to the point where the gut is entirely lost. Morphological evidence from fossils suggests that the symbiosis is ancient in solemyids (Pojeta 1988; Cope 1996a), with the unusual features of the family, compared with the Nuculidae sister group, resulting from a long co-evolutionary history with symbiotic bacteria. Studies on *Solemya velum* and *S. reidi* show that the bivalves live in U and Y shaped mucus-lined burrows with a vertical tube reaching deeply into the anoxic zone (Stanley 1970; Reid 1980). By contrast with Lucinidae, the solemyids are more dynamic in behaviour, actively moving up and down within the burrows between the oxidised and sulphide-rich, anoxic sediment zones. The cylindrical shape, flexible shell, thick shiny periostracum and prehensile, digitate foot coupled with swimming ability may be considered as adaptations to this unusual and ancient lifestyle.

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